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INTERGENERIC HYBRIDS OF TRITICUM AND SECALE WITH HAYNALDIA VILLOSA[1]

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INTRODUCTION

In recent years, particularly during the last decade, considerable effort has been directed by various investigators to the hybridization of the genus *Triticum* with the closely related genera *Aegilops*, *Secale*, *Haynaldia*, and *Agropyron*. This has been done to extend the knowledge on their genetics and cytology, to supply possible information on the phylogenesis of *Triticum*, and to determine further the economic possibilities of intergeneric and interspecific hybridization.

The early literature involving hybridizations of *Triticum*, *Aegilops*, and *Secale* has been reviewed by Bleier (*1*),[2] Kajanus (*3*), Watkins (*12*), Longley and Sando (*4*), and others. More recently Oehler (*5*) has published an extensive paper on crosses of *Triticum* with *Aegilops*. Of the 5 genera, i. e., *Triticum*, *Aegilops*, *Secale*, *Haynaldia*, and *Agropyron*, the last 2 have received less attention by investigators.

Haynaldia has been classified botanically under *Triticum*, *Secale*, and *Agropyron* and as an independent genus. The writer considers, however, that *Haynaldia* is differentiated from *Triticum*, *Secale*, *Aegilops*, and *Agropyron* by characters of sufficient taxonomic importance to be considered a separate genus.

As early as 1914 Raineri (*6*) reported the production by Strampelli in Italy of hybrids between *Triticum villosum* (*Haynaldia*) and *Triticum*. Tschermak (*7*, *8*, *9*) also obtained hybrids between *T. villosum* and several species of *Triticum*, one of which (*T. villosum* × *T. turgidum*) was fertile.

Bleier (*2*), Tschermak (*8*, *9*), Tschermak-Seysenegg (*10*), and Oehler (*5*) reported hybrids between *Triticum villosum* and *Aegilops*. Only recently (1933) Verushkine and Shechurdine (*11*) reported the hybridization of *Triticum* with *Agropyron*.

The present paper records results from the hybridization of *Haynaldia villosa* (L.) Schur. with different species of *Triticum* and with *Secale fragile* L. Illustrations of the parents and hybrids, together with detailed morphological descriptions, illustrations, and data on fertility, are also presented.

[1] Received for publication July 11, 1935; issued January 1936.
[2] Reference is made by number (italic) to Literature Cited, p. 799.

MATERIAL AND METHODS

The seed of *Triticum dicoccoides* Koern., *T. dicoccum* Schrank, *T. durum* Desf., *T. turgidum* L., *T. polonicum* L., *T. vulgare* Vill.,[3] *T. compactum* Host, *T. spelta* L., and *Secale cereale* L. were obtained from the collection of the Division of Cereal Crops and Diseases, Bureau of Plant Industry, United States Department of Agriculture. The seed of *T. aegilopoides* Forsk., *T. timopheevi* Zhuk., *Secale fragile*, *S. cereale* subsp. *ancestrale* Zhuk., and *Haynaldia villosa* were obtained from Dr. P. M. Zhukovsky, of the Bureau of Applied Botany and Genetics, Union of Soviet Socialist Republics.

The crosses herein reported were made in the spring of 1930 in a greenhouse on the Arlington Experiment Farm, near Washington, D. C., and the parental and hybrid plants were likewise grown there. Preparatory to hybridization several upper and lower spikelets on a head were excised before blooming. Emasculation of the remaining flowers was then effected and the head enclosed in a glassine bag. Several days later when the stigmas had reached the stage of receptivity the glassine bags were removed and pollinations made, after which the glassine bags were again replaced until maturity. *Haynaldia villosa* was used as the pollen parent only in all of the crosses herein recorded.

To avoid unfair comparisons of characters subject to variation when plants are grown under different environments, all of the parents and hybrids were grown together in the same greenhouse in 6-inch unglazed earthen pots filled with a uniform mixture of composted soil during the same period of a single year.

Table 1 gives a list of the crosses and the results obtained.

TABLE 1.—*Crosses made with Haynaldia villosa as the male parent, and results obtained*

Female parent	Flowers pollinated	Seeds obtained	Seeds sown	Plants obtained
	Number	*Number*	*Number*	*Number*
Triticum aegilopoides	160	41	10	9
T. timopheevi	64	4	2	2
T. dicoccoides var. *spontaneonigrum*	116	20	17	7
T. dicoccum var. Khapli	188	14	5	1
T. dicoccum var. Black Winter	32	0	0	0
T. durum var. Arnautka	110	14	5	5
T. durum var. Mindum	96	8	3	1
T. durum var. Kubanka	82	15	7	3
T. turgidum var. Alaska	156	69	18	15
T. polonicum var. C. I. 7498 [1]	140	13	5	2
T. vulgare var. C. I. 6223 [1]	325	8	8	[2] 1
T. vulgare var. Hard Federation	90	0	0	0
T. vulgare var. Velvet Chaff	120	0	0	0
T. vulgare var. Nittany	400	1	1	0
T. compactum var. Coppei	130	2	2	0
T. spelta var. Alstroum	95	0	0	0
Secale cereale var. Abruzzes	148	0	0	0
S. cereale subsp. *ancestrale*	80	0	0	0
S. fragile	70	35	14	7

[1] Accession number of Division of Cereal Crops and Diseases.
[2] Died before formation of third leaf.

The more gross characters were studied by simple inspection, while the less gross, such as trichomes, required the use of a binocular dissecting microscope accurately to record form and dimensions. Because of the great variation in their length, diameter, and distribution the trichomes were studied in considerable detail. To differen-

[3] According to the rules of botanical nomenclature the name of this species is *Triticum aestivum* L., but as *T. vulgare* is in general use among agronomists, cereal pathologists, and geneticists, the writer gives preference to the latter form.

tiate the variations of more or less similar morphological structures the terms used in this paper are defined as follows:

A *trichome* is any epidermal hair structure.

A *papilla* is a minute, usually slightly pointed beadlike protuberance 0.02 to 0.05 mm at its greatest diameter and 0.02 to 0.05 mm in perpendicular extension. The small papillae shown in plate 1, *A*, were found on the exterior surfaces of the glumes and lemmas of various species of *Triticum* and *Secale*. The large papillae shown in plate 1, *B*, are 0.025 to 0.05 mm in diameter and 0.02 to 0.05 mm in length and were found on the glumes and lemmas of *Haynaldia villosa*. Plate 2, *D*, shows large papillae found on the lemmas of *Haynaldia villosa*.

An *asperite* is a short, tapering, rigid antrorse point or sharp protruberance. The asperites shown in plate 1, *C*, are 0.03 to 0.2 mm in diameter and 0.06 to 0.5 mm in length and were found on the awns and on the exterior surfaces of the glumes, lemmas, and leaf edges of species of *Triticum*, *Secale*, and *Haynaldia*. Plants bearing small asperites or rigid antrorse points are designated scabrid.

A *spur asperite* is a large asperite which resembles in shape the horny appendage on the leg of a cock. The spur asperites shown in plate 1, *D*, are 0.07 to 0.3 mm in diameter and 0.5 to 1.6 mm in length and are found on the keels of lemmas of *Secale* species. Plants bearing spur asperites are designated scabrous.

A *superasperite* is a greatly enlarged asperite, 0.05 to 0.2 mm in diameter and 0.6 to 3 mm long. Superasperites are found on the glumes of *Triticum polonicum*, *T. timopheevi*, and the F_1 hybrids resulting from the hybridizing of *Haynaldia* with all of the species of *Secale* and *Triticum* except *T. polonicum*. Plate 1, *E*, shows superasperites produced on the glume and lemma keels of an F_1 hybrid resulting from the crossing of *T. turgidum*, which possesses asperites on its glume and lemma keels like those shown in plate 1, *C*, with *H. villosa*, which possesses bristles on its glume and lemma keels like those shown in plate 1, *G*. Plate 1, *F*, shows superasperites produced on the lemma keels of hybrids between *S. fragile*, which possesses asperites on its lemma keels like those shown in plate 1, *D*, and *H. villosa*, which possesses bristles on its lemma keels like those shown in plate 1, *G*.

A *bristle* is a stiffish, resilient, acicular process 0.02 to 0.05 mm in its greatest diameter and 0.2 to 5.0 mm in length. It is usually thicker in the middle than at either end. The bristles illustrated in plate 1, *G*, are 0.02 to 0.05 mm in diameter and 0.2 to 5.0 mm in length and are found on the lateral edges of the rachis internodes and usually in a tuft at the base of the spikelets of species of *Triticum*, *Secale*, and *Haynaldia*. They are also present in tufts on the keel of the glume and apex of the lemma of *Haynaldia*.

A *hair* is a slender flexible process 0.015 to 0.1 mm in diameter and 0.1 to 6.0 mm in length. From its greatest diameter at the base it tapers to a point. Hairs 0.25 to 5 mm in length and 0.03 to 0.09 mm in width are found on the auricles of species of *Triticum*, *Secale*, and *Haynaldia*. The hairs illustrated in plate 1, *H*, are 6 mm long and 0.07 to 0.09 mm in diameter at the base. These long hairs are found on the auricles of hybrids of *T. polonicum* and *T. timopheevi* with *H. villosa*. The hairs illustrated in plate 1, *I*, are 0.02 to 0.04 mm in diameter and 0.7 to 1.7 mm in length and are located on the lodicules, edges, and upper and lower surfaces of the leaf blades and the edges and exterior surfaces of the leaf sheaths of *Triticum*, *Haynaldia*, and *Secale*. The hairs shown in plate 1, *J*, are 0.015 to 0.03 mm in diameter and 0.1 to 0.2 mm long and are found on the leaves and nodes of some species of *Triticum*. This type of hairiness is referred to as puberulence. The hairs illustrated in plate 1, *K*, are 0.015 to 0.03 mm in diameter and 0.3 to 0.7 mm in length and may usually be observed on the exterior surfaces of the glumes, lemmas, and paleas of certain varieties of *Triticum* and *Secale*. This type of hairiness is referred to as pubescence.

THE PARENTS

HAYNALDIA VILLOSA

The plants of *Haynaldia villosa* have an upright habit of growth and in the writer's cultures have attained an average height at maturity of 124.5 cm. The culms are hollow at a point 2.5 cm below the head, glaucous, glabrous, and purple-pigmented (pl. 2, *A*; pl. 3, *C*). The nodes are glabrous.

The leaf blades are 7 mm wide and covered on the upper and lower surfaces with soft hairs 0.5 to 1 mm long. The edges of the leaf blades are scabrid and beset with hairs 1 to 2 mm long. The leaf sheaths are striate, usually weakly purple-pigmented, glaucous, and glabrous. One plant was observed with a trace of hairs on one leaf sheath. No hairs are present on the overlapping edges of the leaf sheaths. The auricles are 1.5 to 2 mm long and are beset with a few hairs 4 mm or less in length. The ligules project 3 mm from the point of attachment to the leaf. No hairs are present on the upper surface of the leaf blade immediately above the ligule (pl. 4, *C*).

The spikes are extremely fragile, 10 to 14 mm wide across the two-ranked face, 7 to 9 cm long, and composed of from twenty to thirty-two 2- to 3-flowered spikelets (fig. 1, *C*). The two lower florets of a spikelet usually produce kernels that average 4.7 mm in length (pl. 2, *H*). At maturity the rachis breaks with a clean fracture at its joints into small segments, at the apex of each of which is attached a spikelet (pl. 5, *C*).

The spikelets are 5 to 6 mm wide and 12 to 15 mm long exclusive of the awns (pl. 5, *C*). On the exterior side of the spikelet at the base are a few short bristles 0.5 mm or less in length (pl. 6, *C*). At the base of the spikelet on the side facing the rachis are also a few short bristles 0.3 mm or less in length (pl. 7, *C*). These bristles sometimes are grouped together, forming a small tuft.

The rachis internodes are obovate, 2 to 3 mm long, and each is glabrous except for a prominent tuft of bristles 1 to 3 mm long, which is located on the lower half of the two lateral edges (pl. 8, *C*).

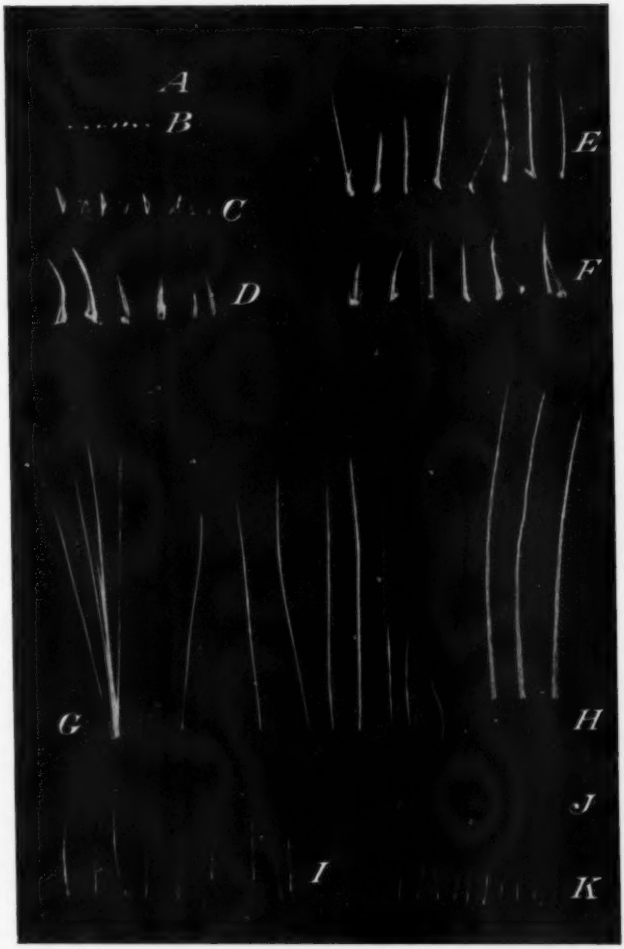
The glumes are glaucous, partly papillate, 1 to 2 mm wide, and 5 to 6 mm long exclusive of the awn and possess four nerves which converge toward the apex of the glume, where they fuse and form a purple scabrid awn 1 to 3 cm long (pl. 5 *C*). The two central nerves form distinct keels that are separated by a longitudinal channel about 1 mm wide at the center (fig. 1, *C*; pl. 5, *C*). Each glume has two keels, which are beset with tufts of bristles 1 to 3 mm long (pl. 5, *C*). The bristles extend upward farther on the front keel and are more abundant than on the rear keel. Sometimes the keels of the glumes may be completely devoid of bristles and possess only asperites or papillae, or both of these may be present together. The glume shoulders are wide, elevated, rounded, and nondentate (pl. 5, *C*).

The lemmas are 2 mm wide, 11 to 13 mm long, and papillate on their convex surfaces. Each has five nerves, the middle one of which forms a keel that terminates in a purple scabrid awn 3 to 4.5 cm long (pl. 5, *C*; pl. 2, *D*). At the apex of the lemma to the right and left of the awn is a short tooth 1 to 2 mm long (pl. 5, *C*). Some of the nerves of the lemma are scabrid. At the apex of the lemma on the keel are several tufts of bristles (pl. 5, *C*).

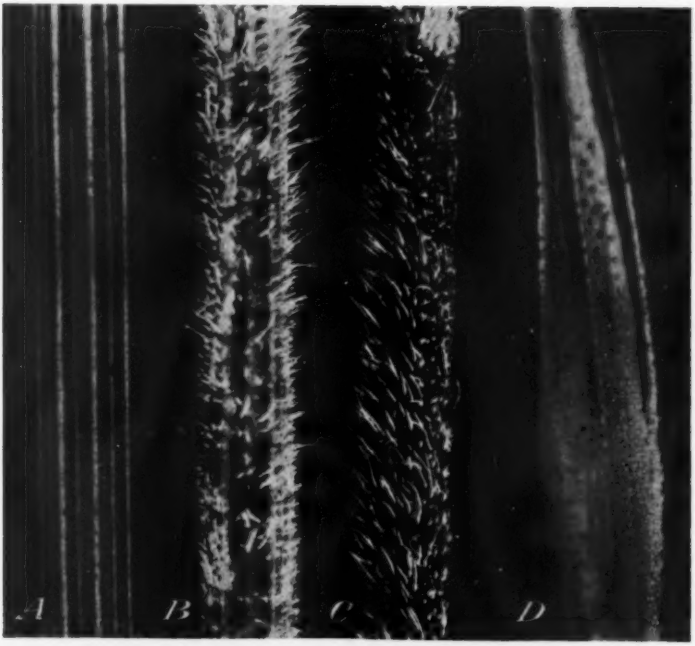
The paleas are entire, not split. The lodicules are 0.9 mm wide and 2 mm long and are beset with hairs 0.05 mm long.

TRITICUM AEGILOPOIDES

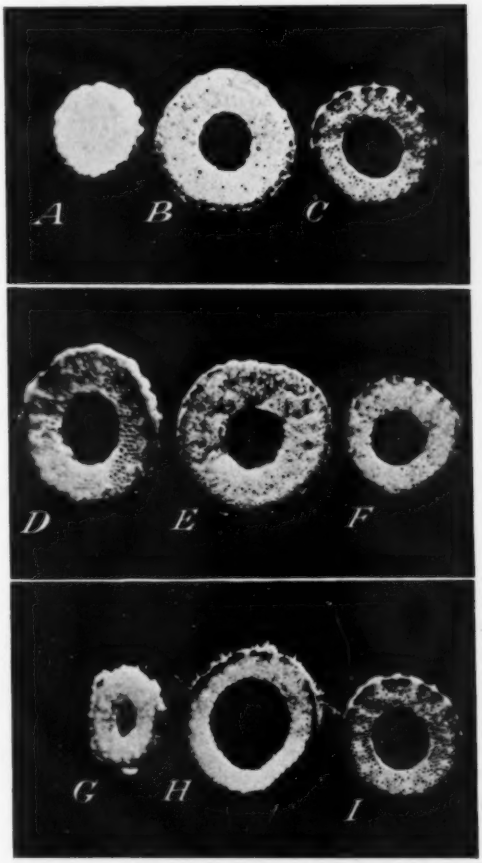
The plants of *Triticum aegilopoides* have an upright habit of growth and attain an average height at maturity of 93 cm. The culms are nonglaucous, without purple pigment, papillate, and solid at a point 2.5 cm below the head (pl. 3, *A*). The nodes are abundantly pubescent with hairs 1 mm or less in length.



Trichomes: *A*, Papillae on glumes and lemmas of *Triticum* and *Secale*; *B*, papillae on glumes and lemmas of *Haynaldia villosa*; *C*, asperites on glumes and lemmas of *Triticum*, *Secale*, and *Haynaldia*; *D*, spur asperites on lemma keels of *Secale*; *E*, superasperites on glume and lemma keels of F_1 hybrids of *T. turgidum* var. Alaska × *H. villosa*; *F*, superasperites on lemma keels of F_1 hybrids of *S. fragile* × *H. villosa*; *G*, bristles on glumes and lemma keels of *H. villosa* and on spikelets at the base and edges of rachis internodes of *Triticum*, *Secale*, and *Haynaldia* spp.; *H*, hairs on auricles of *H. villosa*, *S. fragile*, and all of the species of *Triticum* used except *T. polonicum*; *I*, hairs on lodicules, leaves, and leaf sheaths of certain species of *Triticum*, *Secale*, and *Haynaldia*; *J*, hairs on leaf blades and nodes of certain species of *Triticum*; *K*, hairs on glumes, lemmas, and paleas of certain varieties of *Triticum* and *Secale*. × 10.



Peduncles: *A*, *Haynaldia villosa*; *B*, F_1 of *Secale fragile* × *H. villosa*; *C*, *S. fragile*. Papillae on lemma: *D*, *Haynaldia villosa*. × about 15. Kernels: *E*, *Triticum turgidum* var. Alaska; *F*, F_1 of *T. turgidum* × *H. villosa*; *G*, F_2 of *T. turgidum* × *H. villosa*; *H*, *H. villosa*. × about 4.



Cross sections of culms at a point 2.5 cm below spike: *A*, *Triticum aegilopoides*; *B*, F_1 of *T. aegilopoides* × *Haynaldia villosa*; *C*, *H. villosa*; *D*, *T. durum* var. *Kubanka*; *E*, F_1 of *T. durum* × *H. villosa*; *F*, *H. villosa*; *G*, *Secale fragile*; *H*, F_1 of *S. fragile* × *H. villosa*; *I*, *H. villosa*. × about 15.

PLATE 4

Portions of leaf blades and sheaths with and without tufts of hairs behind ligules: *A*, *Secale fragile*; *B*, F_1 of *S. fragile* × *Haynaldia villosa*; *C*, *H. villosa*. × about 15.

FIGURE 1.—Spikes: *A, Triticum aegilopoides; B,* F_1 *of T. aegilopoides* × *Haynaldia villosa; C, H. villosa.* Natural size.

The leaf blades are 5 mm wide and covered on the upper and lower surfaces with soft hairs 0.5 to 1 mm long. The margins of the leaves are scabrid and beset with hairs 1 to 1.5 mm long. The leaf sheaths are pubescent, nonglaucous, without purple pigment, and the overlapping edges are beset with many hairs 1 to 1.5 mm long. The hairs on the overlapping edge of the upper leaf sheaths are few or entirely absent. The auricles are 1 mm long with hairs 3 to 5 mm in length. The ligules project 1 mm from the point of attachment to the leaf.

The spikes are extremely fragile, laterally compressed, 5 mm wide across the two-ranked face, and 7 to 9 cm long exclusive of awns, and consist of from twenty to forty 2-flowered spikelets (fig. 1, *A*). Each spikelet produces a very small laterally compressed kernel. At maturity the rachis breaks with a clean fracture at its joints into small segments, at the apex of each of which is attached a spikelet (pl. 5, *A*).

The spikelets are 2.5 to 2.8 mm wide and 9 mm long, exclusive of awns (pl. 5, *A*). On the exterior side of the spikelet at its base is a prominent tuft of bristles which are 0.5 to 3.0 mm long (pl. 5, *A*). At the base of the spikelet on the side facing the rachis is a small tuft of hairs which are 0.5 mm or less in length.

The rachis internodes are oblong, 2.7 mm long, and glabrous except on the two lateral edges, which are fringed with numerous bristles 0.5 to 3.0 mm long (pl. 5, *A*).

The glumes are nonglaucous, 1 mm wide, 5 to 7 mm long exclusive of beaks, papillate on their convex surfaces, and possess 4 or 5 nerves, 2 of which are prominent and beset with asperites 0.15 mm in length. The rear one of the 2 prominent nerves forms a keel that terminates in a short beak 1.5 mm long (pl. 5, *A*). At the apex of the front nerve is a short, pointed tooth 0.5 mm long (pl. 5, *A*). The glume shoulders are narrow and oblique, with a sharp-pointed tooth (pl. 5, *A*).

The lemmas are 1.5 to 1.8 mm wide, 7 to 9 mm long exclusive of the awns, 8- to 10-nerved, partly keeled, and abundantly papillate on their convex surfaces. At the apex of each are two prominent scabrid points or teeth 1 mm long, between which is a long, yellow, scabrid awn 2.0 to 9.0 cm long (pl. 5, *A*).

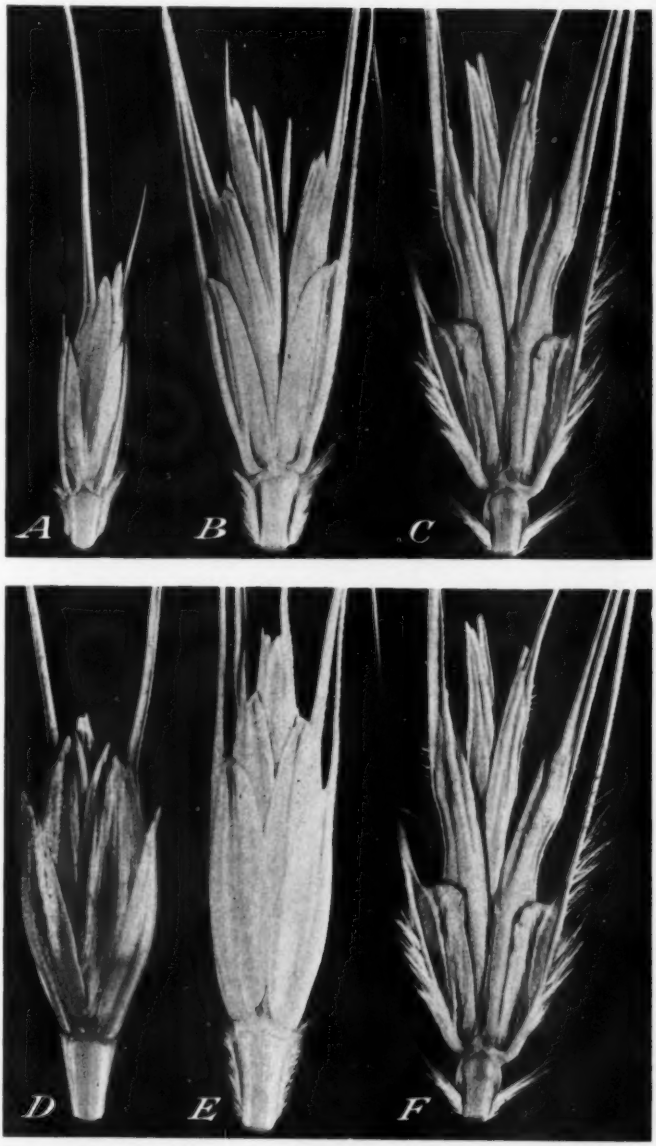
The paleas of the fertile florets are split longitudinally through the middle from the apex to the base.

The lodicules are 0.33 mm wide and 0.8 mm long and are beset with hairs 0.33 mm long.

TRITICUM TIMOPHEEVI

The plants of *Triticum timopheevi* have an upright habit of growth and attain an average height at maturity of 142.2 cm. The culms are glaucous, devoid of purple pigment, and papillate for a distance of several centimeters below the head. The culms are hollow at a point 2.5 cm below the head. The nodes are puberulent, the hairs being 1 mm or less in length. The puberulence may extend 3 mm below the node.

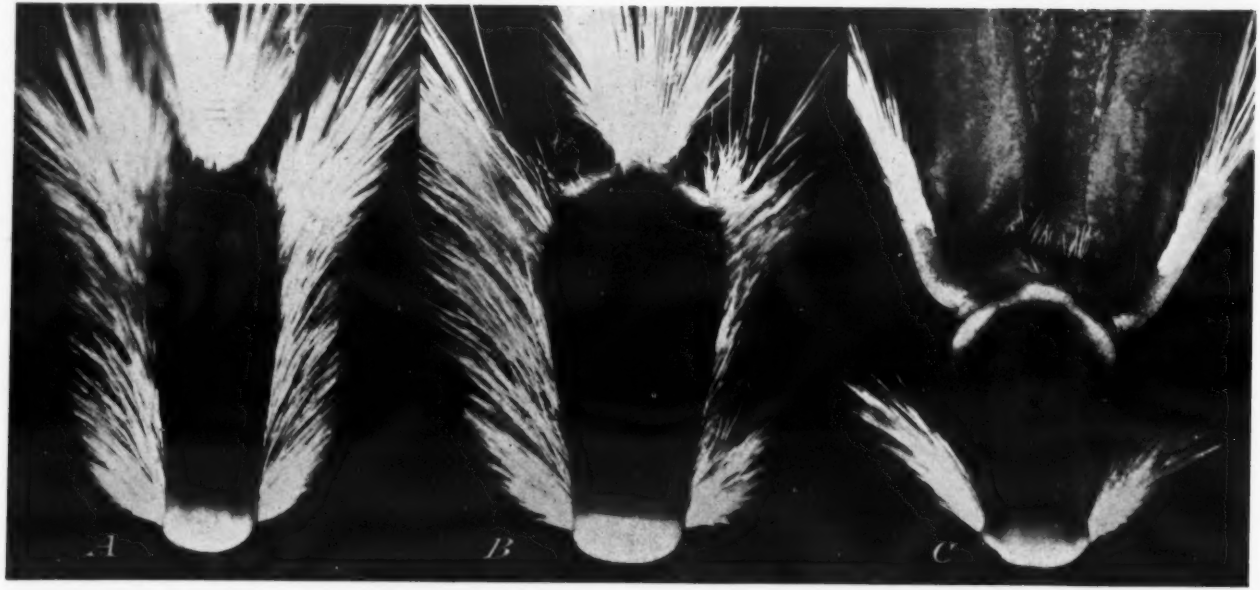
The leaf blades are 8 mm wide, slightly scabrid, and covered on the upper and lower surfaces with hairs 2.5 mm or less in length. The edges of the blades are scabrid and possess hairs 2 mm or less in



Spikelets: *A*, *Triticum aegilopoides*; *B*, *T. aegilopoides* × *Haynaldia villosa*; *C*, *H. villosa*; *D*, *T. dicoccum* var. Khapli; *E*, F_1 of *T. dicoccum* × *H. villosa*; *F*, *H. villosa*. × about 4.

Basal bristles on exterior side of spikelet: *A*, *Triticum dicoccoides* var. *spontaneonigrum*; *B*, F_1 of *T. dicoccoides* × *Haynaldia villosa*; *C*, *H. villosa*. × about 15.

Basal bristles on side of spikelet facing rachis: *A*, *Triticum dicoccoides* var. *spontaneonigrum*. *B*, F_1 of *T. dicoccoides* × *Haynaldia villosa*. *C*, *H. villosa*. × about 15.



Rachis internodes: *A*, ***Triticum dicoccoides*** **var.** ***spontaneonigrum;*** *B*, F_1 of *T. dicoccoides* × *Haynaldia villosa; C, H. villosa.* × about 15.

length. The leaf sheaths are without anthocyanin pigment, glaucous, and usually scabrid. The upper leaf sheaths usually are devoid of hairs, while the lower ones may possess them in abundance 2 mm or less in length. The overlapping edge of each leaf sheath is scabrid and beset with hairs. The auricles are 1 mm long and beset with several hairs 5 mm or less in length. The ligules project 1 mm from the point of attachment to the leaf.

The spikes are 11 to 13 mm wide across the two-ranked face, 6 to 8 cm long exclusive of the awns, and composed of from eighteen to twenty-one 2- or 3-flowered spikelets (fig. 2, *A*). At maturity, the head may break at the base as a unit just above the uppermost sterile spikelet (pl. 9, *D*). However, with slight pressure the rachis breaks with a slightly ragged fracture into small segments, at the apex of each of which is attached a spikelet.

The spikelets are 7 to 8 mm wide and 16 to 18 mm long exclusive of the awns or beaks (pl. 9, *D*). Each spikelet usually contains two slender kernels. On the exterior side of the spikelet at the base is a prominent tuft of bristles, which are 2 mm or less in length and extend to the fringed edges of the rachis internodes to which the spikelet is attached (pl. 9, *D*). At the base of the spikelet on the side facing the rachis is a smaller tuft of bristles which are 1 mm or less in length.

The rachis internodes are 2 mm long, partly puberulent, and papillate on the convex and concave surfaces, and the edges are fringed with numerous bristles 1 mm or less in length (pl. 9, *D*).

The glumes are 2 to 3 mm wide, 9 mm long exclusive of the awns, densely pubescent, and glaucous, and each possesses 5 to 7 nerves, the most prominent one of which forms the keel, which is beset on its upper edges with asperites 0.5 mm or less in length (pl. 9, *D*). Some of the hairs on certain portions of the glume, especially on the keel and other prominent nerves, are thicker and longer than the others. These thick hairs resemble superasperites and attain a maximum length of 1 mm. The keel is very sharp and is terminated by a beak 5 mm or less in length. The glume shoulders are narrow, with a pointed tooth (pl. 9, *D*).

The lemmas are 3 to 3.5 mm wide, 13 to 14 mm long exclusive of the awns, pubescent on exposed portions, and papillate on portions covered by the glumes. They possess 8 to 9 inconspicuous nerves, the central one of which is partly keeled and terminates in a brown to black scabrid awn 11 cm or less in length. The hairs on the lemma at the apex may vary in length and thickness. These long hairs resemble superasperites and attain a maximum length of 1 mm.

The paleas are entire, not split. The lodicules are 0.6 mm wide and 1.8 mm long and are beset with hairs 0.65 mm long.

TRITICUM DICOCCOIDES

The plants of *Triticum dicoccoides* var. *spontaneonigrum* have an upright habit of growth and attain an average height at maturity of 76.2 cm. The culms are not glaucous, solid at a point 2.5 cm. below the head, and without purple pigment. The nodes are abundantly covered with deflexed hairs 0.2 to 0.4 mm long.

The leaf blades are 6 to 8 mm wide and puberulent on the upper and lower surfaces. The edges of the leaf blades are slightly

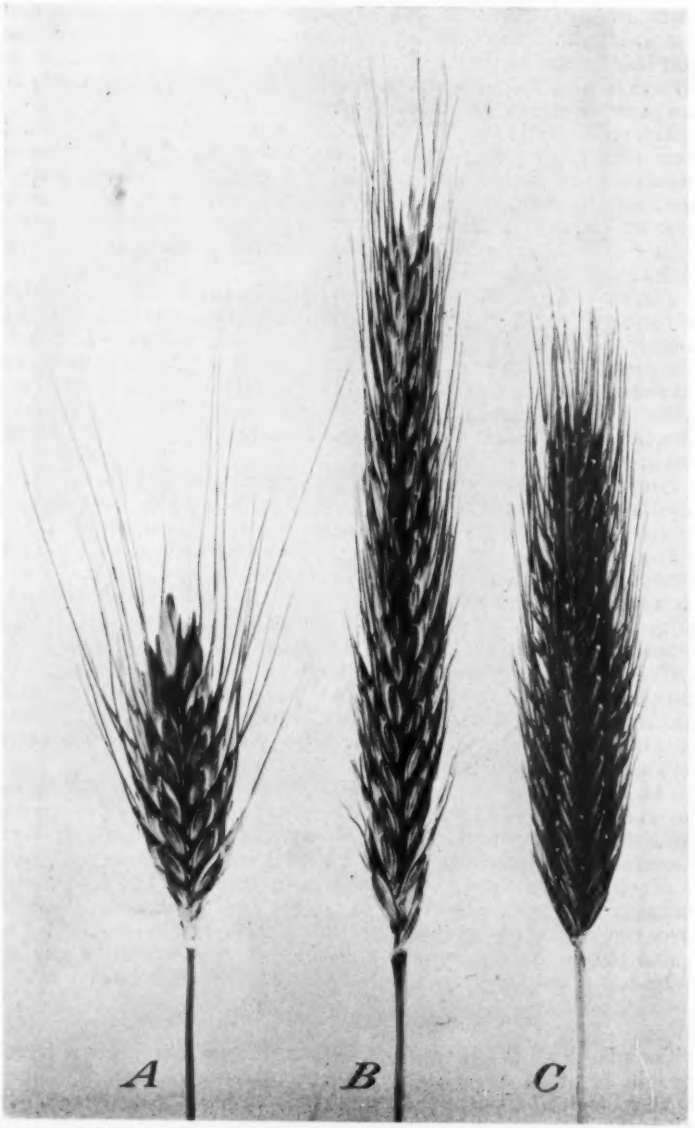


FIGURE 2.—Spikes: *A, Triticum timopheevi; B,* F_1 *of T. timopheevi* × *Haynaldia villosa; C, H. villosa.* Natural size.

scabrid and devoid of hairs. The leaf sheaths are nonglaucous, without purple pigment, and glabrous except on the edges, which are fringed with hairs. The auricles are 1 mm long and are beset with hairs 2 to 3 mm long. The ligules project about 3 mm from the point of attachment to the leaf.

The spikes are extremely fragile, laterally compressed, 8 to 9 mm wide across the two-ranked face, and 7 to 9 cm long exclusive of the awns, and consist of from sixteen to eighteen 2- or 3-flowered spikelets, each of which normally contains two kernels (fig. 3, *A*). At maturity the rachis disarticulates at its joints with a clean fracture into small segments at the apex of each of which is attached a spikelet (pl. 10, *A*).

The spikelets are 4 to 5 mm wide and 15 to 17 mm long exclusive of the awns. On the exterior side of the spikelet at the base is a conspicuous tuft of bristles 3 to 5 mm long (pl. 6, *A*). At the base of the spikelet on the side facing the rachis is a small tuft of bristles 2 mm or less in length (pl. 7, *A*).

The rachis internodes are nonglaucous, oblong, 4 mm long, and glabrous except on the two lateral edges, which are fringed along their entire length with numerous bristles 0.5 to 5 mm long (pl. 8, *A*).

The glumes are nonglaucous, 2 mm wide, 12 to 13 mm long exclusive of the beak, and white with black streaks which sometimes appear as a solid mass of black pigment (pl. 10, *A*). They possess two prominent nerves, the rear one of which is beset with large asperites, is papillate, and forms a keel that terminates in a short beak 2 mm long, while at the apex of the forward nerve is a very short tooth less than 0.25 mm long (pl. 10, *A*). One or two less conspicuous nerves may be present also on the glumes. The glume shoulders are narrow and oblique, with a very short, pointed tooth (pl. 10, *A*).

The lemmas are 2 mm wide, 14 to 15 mm long exclusive of the awn, partly papillate, and slightly scabrid on their exposed surfaces. Each terminates in three points, the center one of which is extended into a scabrid, black awn, 10 to 17.5 cm long (pl. 10, *A*).

The paleas are entire, not split. The lodicules are 0.9 mm wide and 1.6 mm long and are beset with hairs 0.6 mm long.

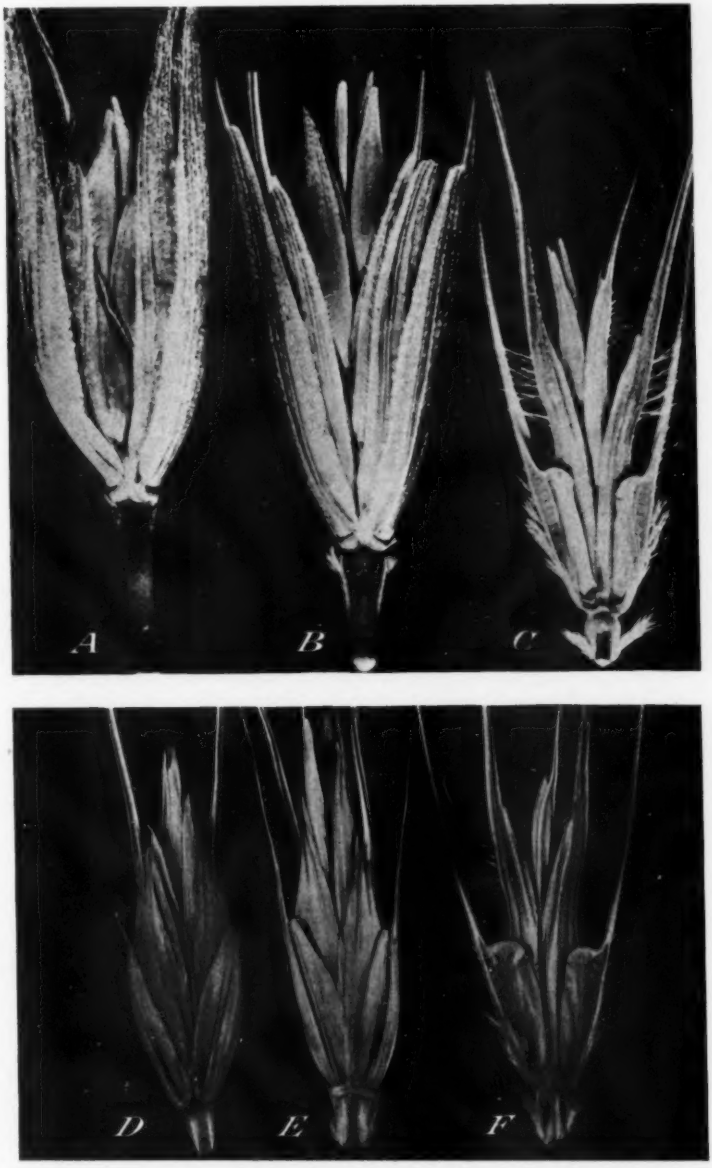
TRITICUM DICOCCUM

The plants of *Triticum dicoccum* var. Khapli have an upright habit of growth and attain an average height at maturity of 68.6 cm. The culms are glabrous, nonglaucous, without purple pigment, and solid at a point 2.5 cm below the head. The nodes are puberulent.

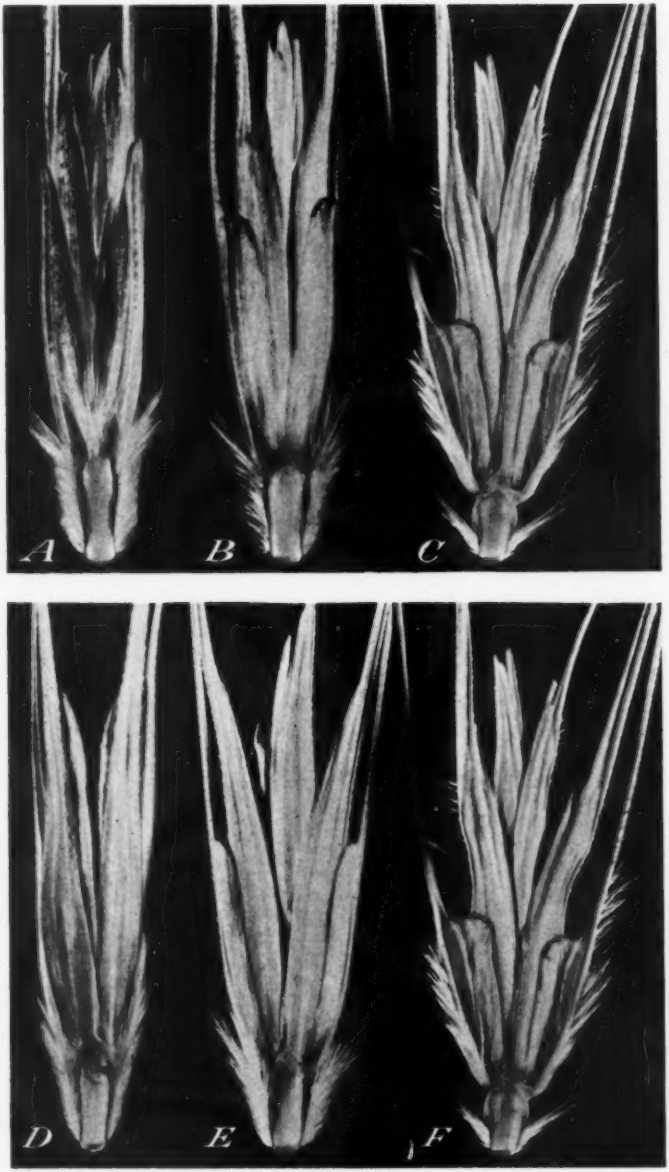
The leaf blades are 10 to 12 mm wide and puberulent on both the upper and lower surfaces. The margins of the leaf blades are scabrid and devoid of hairs. The leaf sheaths are slightly glaucous, without purple pigment, and glabrous on the exterior surfaces, while the lateral edges of the sheaths are devoid of hairs. The auricles are 1.5 to 2.0 mm long with a few hairs 0.7 mm or less in length. The ligules project 2.0 mm from the point of attachment to the leaves.

The spikes are fragile, laterally compressed, 8 to 10 mm wide across the two-ranked face, 7 to 9 cm long, and consist of from sixteen to twenty-four 2- or 3-flowered spikelets, each of which normally produces two kernels (fig. 4, *A*). At maturity the rachis usually breaks with an imperfect or ragged fracture at its joints into small segments, at the apex of each of which is attached a spikelet (pl. 5, *D*).

FIGURE 3.—Spikes: *A, Triticum dicoccoides* var. *spontaneonigrum; B,* F_1 *of T. dicoccoides* × *Haynaldia villosa; C, H. villosa.* Natural size.

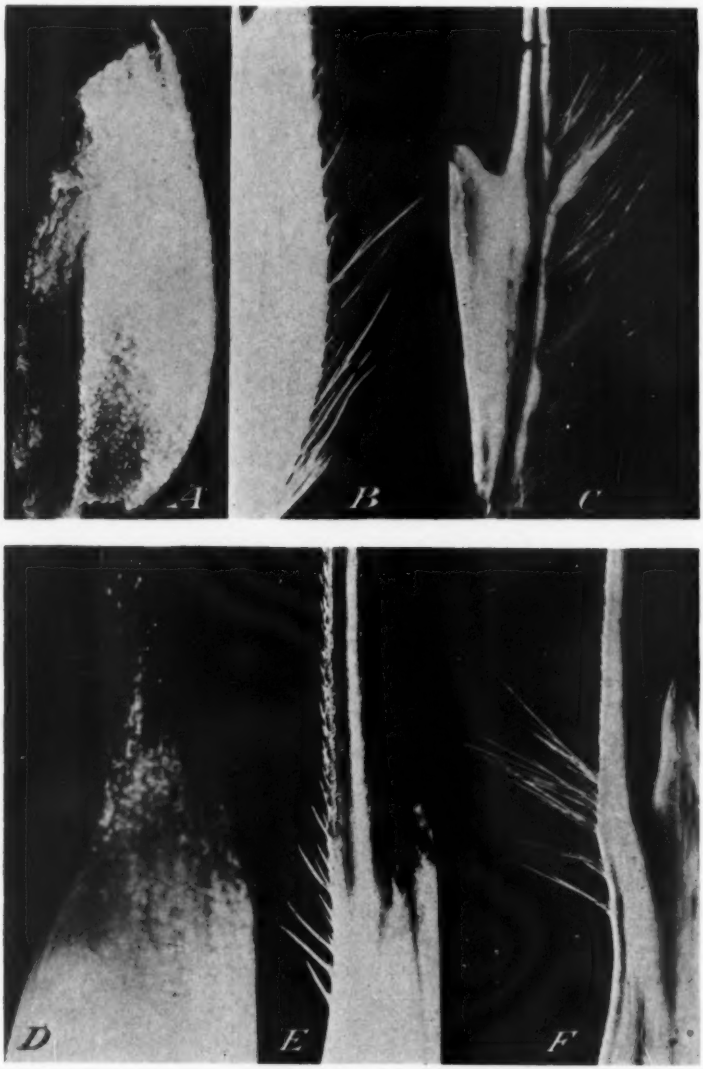


Spikelets: *A*, *Triticum polonicum* (C. I. 7498); *B*, F_1 of *T. polonicum* × *Haynaldia villosa*; *C*, *H. villosa*; *D*, *T. timopheevi*; *E*, *T. timopheevi* × *H. villosa*; *F*, *H. villosa*. × about 3.



Spikelets: *A, Triticum dicoccoides* var. *spontaneonigrum; B,* F_1 of *T. dicoccoides* × *Haynaldia villosa; C, H. villosa; D, Secale fragile; E,* F_1 of *S. fragile* × *H. villosa; F, H. villosa.* × about 4.

Spikelets: *A*, *Triticum turgidum* var. Alaska; *B*, F_1 of *T. turgidum* × *Haynaldia villosa*; *C*, *H. villosa*; *D*, *T. durum* var. Kubanka; *E*, F_1 of *T. durum* × *H. villosa*; *F*, *H. villosa*. × about 3.



Glumes: *A*, *Triticum turgidum* var. Alaska; *B*, F_1 of *T. turgidum* × *Haynaldia villosa*; *C*, *H. villosa*. × about 12. Lemmas: *D*, *Triticum turgidum* var. Alaska; *E*, F_1 of *T. turgidum* × *Haynaldia villosa*; *F*, *H. villosa*. × about 12.

The spikelets are 6 to 7 mm wide and 10 to 11 mm long exclusive of the awns (pl. 5, *D*). On the exterior side of the spikelet at the base is a prominent tuft of bristles which are 1 to 1.25 mm long (pl. 5, *D*). At the base of the spikelet on the side facing the rachis is also a small tuft of bristles which are 0.25 to 0.8 mm long.

The rachis internodes are weakly glaucous, 3 mm long, and glabrous except on the two lateral edges, which are fringed with numerous bristles 0.25 to 1 mm long (pl. 5, *D*).

The glumes are weakly glaucous, 2.5 mm wide, 9 to 10 mm long exclusive of the beak, papillate on their convex surfaces, and possess 6 to 7 nerves, two of which appear prominent. Of the 2 to 3 prominent nerves on each glume, the one nearest to the rachis forms a sharp keel which terminates in a short beak 0.5 mm long (pl. 5, *D*). The upper half of the keels is beset with short asperites, the lower portion being papillate. Occasionally the upper portion of the other prominent nerves are slightly scabrid. The glume shoulders are narrow and oblique, with a short, blunt tooth.

The lemmas are 3 mm wide and 10 to 11 mm long, 10 to 11 nerved, and papillate on their convex surfaces. At the apex of each lemma are two teeth or points less than 0.5 mm long between which is a yellow scabrid awn 3 to 9 cm long (pl. 5, *D*).

The paleas are entire, not split. The lodicules are 0.9 mm wide and 1.7 mm long and are beset with hairs 0.6 mm long.

TRITICUM DURUM

The plants of *Triticum durum* var. Kubanka have an upright habit of growth and attain an average height at maturity of 132 cm. The culms are glabrous, glaucous, without purple pigment, and hollow at a point 2.5 cm below the head (pl. 3, *D*). The nodes are glabrous.

The leaf blades are 8 to 10 mm wide and glabrous on the upper and lower surfaces. The edges of the leaf blades are scabrid and devoid of hairs. The leaf sheaths are glaucous, without purple pigment, glabrous on the exterior surfaces, and devoid of hairs on the lateral edges. The auricles are 1 to 2 mm long and devoid of hairs. The ligules project 2 to 2.5 mm from the point of attachment to the leaf.

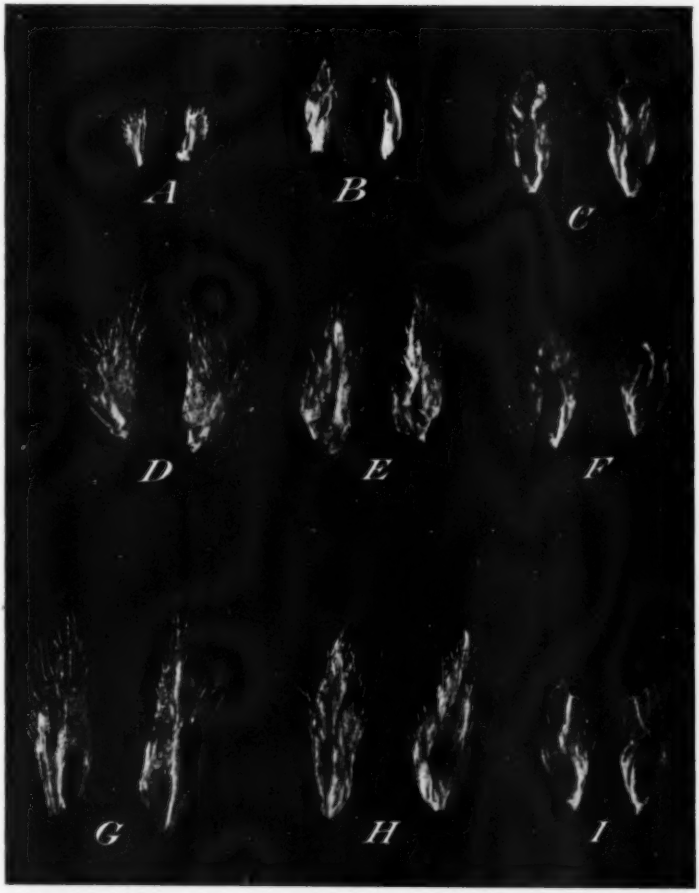
The spikes are nonfragile, 7 to 8 mm wide across the two-ranked face, 7 to 8 cm long, and composed of from eighteen to twenty-four 2- to 4-flowered spikelets, each of which usually contains two kernels (fig. 5, *A*).

The spikelets are 10 to 12 mm wide and 12 to 14 mm long exclusive of the awns. On the exterior side of the spikelet at the base is a tuft of bristles 2 mm or less in length. At the base of the spikelet on the side facing the rachis is a tuft of bristles 0.3 mm or less in length.

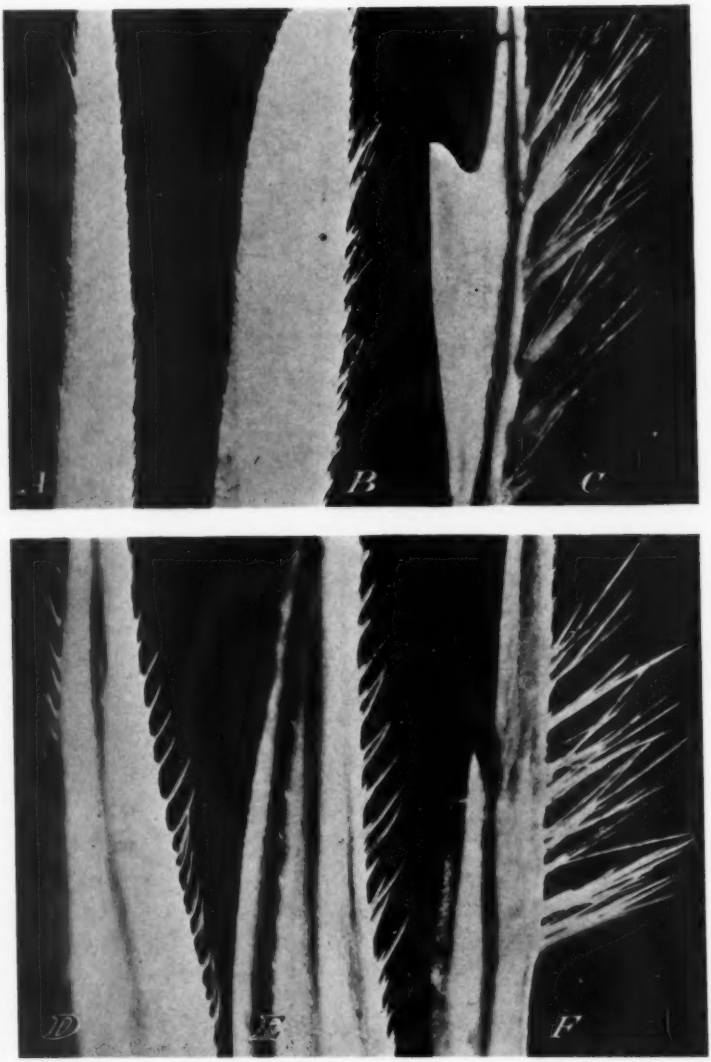
The rachis is continuous. The rachis internodes are 3 to 5 mm long, partly glaucous, and glabrous except on the two lateral edges, which are fringed with short bristles 0.2 to 0.3 mm long near the base and 1 to 1.5 mm at the apex.

The glumes are 1.5 to 2 mm wide and 7 to 8 mm long exclusive of beak, papillate, glaucous on their convex surfaces, and possess 7 to 8 nerves, the most prominent of which forms a scabrid keel which

FIGURE 4.—Spikes: *A, Triticum dicoccum* var. Khapli; *B*, F_1 of *T. dicoccum* × *Haynaldia villosa*; *C*, *H. villosa*. Natural size.



Lodicules: *A*, *Triticum aegilopoides*; *B*, F_1 of *T. aegilopoides* × *Haynaldia villosa*; *C*, *H. villosa*; *D*, *T. polonicum* (C. I. 7498); *E*, F_1 of *T. polonicum* × *H. villosa*; *F*, *H. villosa*; *G*, *Secale fragile*; *H*, F_1 of *S. fragile* × *H. villosa*; *I*, *H. villosa*. × 12½.



Glumes: *A*, *Secale fragile*; *B*, F_1 of *S. fragile* × *Haynaldia villosa*; *C*, *H. villosa*. Lemmas: *D*, *S. fragile*; *E*, F_1 of *S. fragile* × *H. villosa*; *F*, *H. villosa*. × about 13.

FIGURE 5.—Spikes: *A, Triticum durum* var. Kubanka; *B*, F_1 *T. durum* × *Haynaldia villosa; C, H. villosa.* Natural size.

terminates in a beak 1 to 2 mm long. The glume shoulders are narrow, slightly elevated, and nondentate (pl. 11, *D*).

The lemmas are 2 to 2.5 mm wide, 8 to 9 mm long exclusive of awns, papillate, glaucous on their upper exposed surfaces, and possess 1 to 13 nerves, the most prominent of which terminates in a yellow scabrid awn 10 to 16 cm long.

The lodicules are 0.9 mm wide and 1.3 mm long and are beset with hairs 0.5 mm long.

TRITICUM POLONICUM

The plants of *Triticum polonicum* (C. I. no. 7498) have an upright habit of growth and attain an average height at maturity of 124.5 cm. The culms are glabrous and hollow, with a small cavity at a point 2.5 cm below the head, glaucous, and without purple pigment. The nodes are puberulent and glaucous.

The leaf blades are 18 to 22 mm wide and practically devoid of hairs on the upper and lower surfaces. The margins of the leaf blades are scabrid and beset with short hairs less than 1 mm in length for a distance of 5 mm above the auricle. The leaf sheaths are glaucous, without purple pigment, glabrous on the exterior surfaces, and usually devoid of hairs. The auricles are 1 mm long with a few hairs 0.4 mm or less in length. The ligules project 1.5 to 2.0 mm from the point of attachment to the leaf.

The spikes are nonfragile, 12 to 14 mm wide across the two-ranked face, 11 to 13 cm long exclusive of the awns, and consist of from eighteen to twenty-two 3- or 4-flowered spikelets, each of which usually contains three long kernels (fig. 6, *A*).

The spikelets are 10 to 12 mm wide and 20 to 25 mm long exclusive of awns (pl. 9, *A*). On the exterior side of the spikelet at the base is a tuft of bristles 0.5 to 2.5 mm long (pl. 9, *A*). At the base of the spikelet on the side facing the rachis is a tuft of bristles 0.3 mm or less in length.

The rachis is continuous. The rachis internodes are 7 to 9 mm long, glaucous, and glabrous except on the two lateral edges, which are partly fringed with bristles 0.5 to 2.0 mm long (pl. 9, *A*).

The glumes are glaucous, 3 mm wide and 22 mm long, and possess 8 to 10 nerves, the most prominent of which forms a keel that terminates in a tooth or beak 1.5 to 5 mm long (pl. 9, *A*). A weaker secondary keel may also be developed. The keels and some of the nerves showing prominence at the apex of the glume are beset with long, slender asperites 0.5 mm or less in length. The convex surface of each glume on the membranous portion of the two wings and on the edge is pubescent (pl. 9, *A*). Other parts of the glume may be papillate or puberulent. The glume shoulders are narrow, elevated, and nondentate (pl. 9, *A*).

The lemmas are 4 mm wide, 20 to 28 mm long, glaucous, papillate, and pubescent on the exposed surfaces (pl. 9, *A*). Each lemma possesses 9 to 12 nerves, the most prominent of which terminates in a partially black, scabrid awn 9 to 12 cm long (fig. 6, *A*).

The paleas are entire, not split. The lodicules are 1 mm wide and 1.6 mm long and are beset with hairs 1.35 mm long.

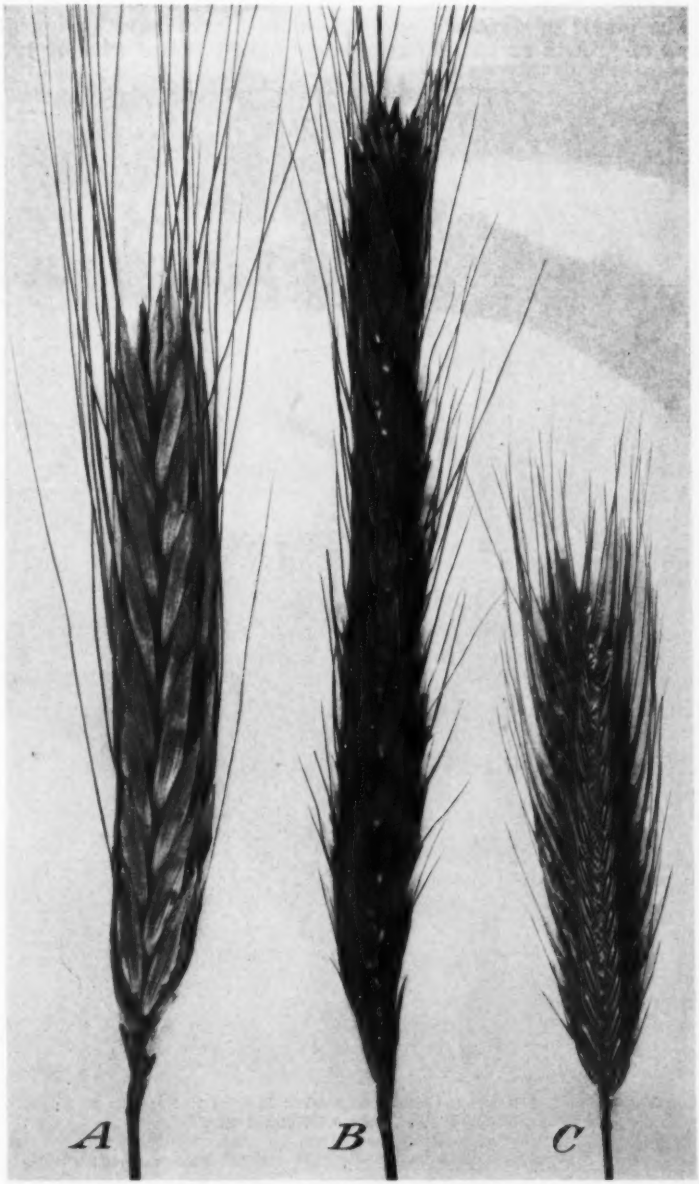


FIGURE 6.—Spikes: *A, Triticum polonicum* (C. I. 7498); *B*, F_1 of *T. polonicum* × *Haynaldia villosa*; *C, H. villosa*. Natural size.

TRITICUM TURGIDUM

The plants of *Triticum turgidum* var. Alaska have an upright habit of growth and attain an average height at maturity of 127.0

FIGURE 7.—Spikes: *A*, *Triticum turgidum* var. Alaska: *B*, F_1 of *T. turgidum* × *Haynaldia villosa*; *C*, *H. villosa*. Natural size.

cm. The culms are glabrous, glaucous, without purple pigment, and solid at a point 2.5 cm below the head. The nodes are glabrous.

The leaf blades are 15 to 18 mm wide and abundantly puberulent on the upper surface, while the lower surface is only sparsely puberulent. The edges of the blades are nonscabrid and free from hairs.

The leaf sheaths are glaucous, without purple pigment, and glabrous on the surface and overlapping lateral edges. The auricles are 2 to 3 mm long and beset with a few short hairs less than 0.25 mm long. The ligules project 3 mm from the point of attachment to the leaf.

The spikes may be branched or simple, nonfragile, 8 to 12 cm long exclusive of the awns, and may vary in width from 12 to 35 mm across the two-ranked face (fig. 7, *A*).

The spikelets are 7 to 8 mm wide, 9 to 10 mm long exclusive of the awns, and generally contain two short plump kernels with a high dorsal arch or hump (pl. 11, *A*; pl. 2, *E*). On the exterior side of the spikelet at the base is a tuft of bristles which are 3.0 mm or less in length and sometimes extend to the edges of the rachis internode to which the spikelet is attached (pl. 11, *A*). At the base of the spikelet on the side facing the rachis is a tuft of short bristles 0.5 mm or less in length.

The rachis is continuous. The rachis internodes are oblong, 2.5 to 3.0 mm long, glaucous, and glabrous, and the edges are fringed with numerous bristles 3 mm or less in length (pl. 11, *A*).

The glumes are 2.5 mm wide, 5 to 6 mm long exclusive of the beaks, papillate, glaucous on their convex surfaces, and possess four prominent nerves, the most conspicuous of which forms the keel and terminates in a short beak 0.5 mm or less in length. The keels throughout the entire length of the glumes are beset with asperites 0.2 mm or less in length (pl. 12, *A*). The exterior surface of the membranous portion of the two wings of the glume is partly puberulent. The glume shoulders are narrow, oblique, and nondentate (pl. 11, *A*).

The lemmas are 3 mm wide, 8 mm long exclusive of the awns, glaucous, slightly scabrid on their upper exposed surfaces, and possess 8 to 11 nerves. The most prominent nerve on each lemma terminates in a scabrid, black awn 6 to 11 cm long (pl. 12, *D*).

The paleas are entire, not split. The lodicules are 0.7 mm wide and 1.1 mm long and are beset with hairs 0.7 mm long.

SECALE FRAGILE

The plants of *Secale fragile* have an upright habit of growth and attain an average height at maturity of 76 cm. The culms are hollow, purple-pigmented, glaucous, and covered with hairs 1 mm or less in length for several centimeters immediately below the head (pl. 2 *C;* pl. 3, *G*). The nodes are puberulent.

The leaf blades are 6 to 7 mm wide and covered with hairs 1 to 1.5 mm long on their upper surfaces. The lower surfaces of the leaf blades are puberulent. The edges of the leaf blades are scabrid and beset with hairs 0.3 mm long for a distance of 5 mm above the auricle on the blade. Just above the ligule on the leaf blade is a prominent collar of hairs that do not exceed 2 mm in length. The upper leaf sheaths are glabrous, glaucous, and slightly purple-pigmented on the exterior surfaces. The lower leaf sheaths are hairy. The lateral edges of the sheaths are devoid of hairs. The auricles are 0.5 mm in length and possess very short hairs 0.4 mm or less in length. The ligules project 0.5 to 0.7 mm above the point of attachment to the leaf.

The spikes are extremely fragile, 7 to 8 mm wide across the two-ranked face, 8 to 11 cm long exclusive of the awns, and consist of

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FIGURE 8.—Spikes: *A*, *Secale fragile*; *B*, F_1 of *S. fragile* × *Haynaldia villosa*; *C*, *H. villosa*. Natural size.

twenty-six to thirty-six 2-flowered spikelets (fig. 8, *A*). Each spikelet usually produces two kernels. At maturity the rachis breaks with a clean fracture at its joints into small segments at the apex of each of which is attached a spikelet (pl. 10, *D*).

The spikelets are 5 mm wide and 14 to 16 mm long exclusive of the awns. On the exterior side of the spikelet at the base are a few extremely short bristles (pl. 10, *D*). At the base of the spikelet on the side facing the rachis are a short tuft and a collar of bristles which are 0.2 mm or less in length. The rachis internodes are 3 to 4 mm long, glaucous, and glabrous, and the two lateral edges are fringed with bristles 4 mm or less in length (pl. 10, *D*).

The glumes are slightly glaucous, subulate-pointed, 0.5 mm wide, 13 to 14 mm long exclusive of a scabrid awn 6 mm long, partly papillate, and scabrid on the exterior surfaces (pl. 10, *D*). Each glume has a keel which is densely beset with slender asperites 0.5 mm or less in length, which become longer and resemble hairs as they approach the base of the glume. The margins of the glumes are fringed with numerous slender hairs 1 mm or less in length. The glumes are sparsely beset with asperites. Glume shoulders are wanting (pl. 10, *D*).

The lemmas are 2.5 mm wide, 15 to 17 mm long exclusive of the awn, papillate, and 3- to 5-nerved; the most prominent nerve forms a keel beset throughout its entire length with somewhat uniformly separated and linearly arranged spur asperites 1 mm or less in length (pls. 1, *D;* 10, *D*). The keel is terminated by a partially purple-pigmented, scabrid awn 12 cm long. The edges of the lemma are beset with hairs 0.5 to 0.7 mm long. The exposed portion of the lemmas on and near the adges and at the apex is usually beset with asperites or spur asperites.

The paleas are entire, not split. The lodicules are 1.1 mm wide and 2.9 mm long and are beset with hairs 1.25 mm long.

THE F_1 HYBRIDS

TRITICUM AEGILOPOIDES × HAYNALDIA VILLOSA

The plants of the *Triticum aegilopoides* × *Haynaldia villosa* hybrid have an upright habit of growth and attain an average height at maturity of 116.8 cm. The culms are glaucous, nonpapillate, hollow at a point 2.5 cm below the head, and purple-pigmented (pl. 3, *B*). The nodes are sparsely puberulent.

The leaf blades are 6 to 7 mm wide and covered on the upper and lower surfaces with hairs 1 to 1.5 mm long. The edges of the leaf blades are scabrid and possess hairs 1.5 to 2 mm long. The leaf sheaths are glaucous, pubescent, slightly purple-pigmented on the exterior surface, and glaucous on the lateral edges. The auricles are 1.5 mm long with hairs 3 mm or less in length. The ligules project 1.5 mm from the point of attachment to the leaf.

The spikes are extremely fragile, 4 to 6 mm wide across the two-ranked face, 9 to 11 cm long exclusive of the awns, and composed of from thirty to forty-six 2- or 3-flowered sterile spikelets (fig. 1, *B*). At maturity the rachis breaks with a clean fracture at its joints into small segments, at the apex of each of which is attached a spikelet (pl. 5, *B*).

The spikelets are 7 mm wide and 11 mm long exclusive of the awns. On the exterior side of the spikelet at the base is a tuft of bristles which are 2 mm or less in length (pl. 5, *B*). At the base of the spikelet on the side facing the rachis is another tuft of bristles, which are 0.5 mm or less in length.

The rachis internodes are 2.5 to 3.0 mm long and glabrous except on the two lateral edges, which are fringed with bristles 0.5 to 3.0 mm long (pl. 5, *B*).

The glumes are glaucous, intermediate in shape between those of the two parents, 1.7 to 2.0 mm wide, 7 to 8 mm long exclusive of the awns, papillate except on the membranous portion near the edges, and each possesses five nerves, the two most prominent of which form keels. The rear keel is the primary or more prominent one of the two and is beset with individually arranged superasperites which are 2.0 mm or less in length. The primary keel of the glume terminates in a scabrid awn 2.0 to 2.5 cm long (pl. 5, *B*). The secondary or forward keel is beset with asperites 0.3 mm or less in length and terminates in a tooth 0.2 mm or less in length (pl. 5, *B*). Between the two keels is a very shallow, longitudinal depression, through the center of which passes laterally a conspicuous nerve which unites with the primary keel at the apex of the glume. The glume shoulders are intermediate between the two parents in width and have a sharp-pointed tooth (pl. 5, *B*).

The lemmas are 2.0 to 2.1 mm wide, 10 to 11 mm long exclusive of the awns, papillate on the exterior surfaces, and each has seven nerves, the middle one of which is partly keeled and terminates in a weakly purple-pigmented, scabrid awn 3.0 to 6.5 cm long. At the apex of the glume on the keel are several superasperites 1.3 mm or less in length (pl. 5, *B*). Some of the less conspicuous nerves located on the exposed portion of the lemma may also be scabrid.

The paleas are entire, not split. The lodicules are 0.5 mm wide and 1.5 mm long and are beset with hairs 0.42 mm long.

TRITICUM TIMOPHEEVI × HAYNALDIA VILLOSA

The plants of the hybrid *Triticum timopheevi* × *Haynaldia villosa* have an upright habit of growth and attain an average height at maturity of 149.86 cm. The culms are glaucous, glabrous, purple-pigmented, and hollow at a point 2.5 cm below the head. The nodes are puberulent with very short hairs.

The leaf blades are 8 to 11 mm wide and are covered on the upper and lower surfaces with hairs 2.5 mm or less in length. The edges of the blades are scabrid and possess hairs 3 mm or less in length. The leaf sheaths are purple-pigmented and glaucous. The upper leaf sheaths of the plant are usually devoid of hairs, while the lower ones may be sparsely covered with hairs. The overlapping lateral edge of each leaf sheath is beset with hairs 2 mm or less in length. The auricles are 1.2 mm long and are beset with several hairs 6 mm or less in length. The ligules project 1.3 mm or less from the point of attachment to the leaf.

The spikes are extremely fragile at maturity, 10 to 12 mm wide across the two-ranked face, 9 to 11.5 cm long exclusive of the awns, and composed of from thirty to thirty-five 3- or 4-flowered sterile spikelets (fig. 2, *B*). At maturity the rachis breaks with a clean

fracture at its joints into small segments, at the apex of each of which is attached a spikelet.

The spikelets are 4.0 to 5.5 mm wide and 16 to 19 mm long exclusive of awns. On the exterior side of the spikelets at the base is a tuft of bristles which are 1 mm or less in length (pl. 9, *E*). At the base of the spikelet on the side facing the rachis is a smaller tuft of bristles, which are 0.5 mm or less in length.

The rachis internodes are 3.0 to 3.5 mm long, sparsely puberulent, and papillate (pl. 9, *E*). The two lateral edges are fringed with bristles 1.5 mm or less in length (pl. 9, *E*).

The glumes are 2.0 to 2.5 mm wide, 8 mm long exclusive of beaks, glaucous, papillate on the exterior surfaces, and possess 5 to 6 nerves, the two most prominent of which are beset with superasperites 1.7 mm or less in length. The exterior surfaces of the glumes are usually devoid of hairs except on the margins of the glumes, which are partly pubescent (pl. 9, *E*). The awns on the glumes are purplish black, scabrid, and 5 cm or less in length. The glume shoulders are intermediate in width between those of the parents, elevated, and nondentate (pl. 9, *E*).

The lemmas are 2.5 to 3.0 mm wide, 12 to 14 mm long exclusive of the awns, papillate on the exterior surface, and partly pubescent on the upper exposed portions. The awns are purplish brown to purplish black. Superasperites usually are not present on the keels of the lemmas, but when present they are usually confined to the keel at the apex of the lemma.

The paleas are entire, not split. The lodicules are 0.8 mm wide and 1.9 mm long and are beset with hairs 0.3 mm long.

TRITICUM DICOCCOIDES × HAYNALDIA VILLOSA

The plants of the hybrid *Triticum dicoccoides* × *Haynaldia villosa* have an upright habit of growth and attain an average height at maturity of 154.9 cm. The culms are glaucous, purple-pigmented, and hollow at a point 2.5 cm below the head. The nodes are puberulent.

The leaf blades are 7 to 8 mm wide and covered on the upper and lower surfaces with hairs 1 to 1.5 mm long. The edges of the blades are scabrid and possess hairs 2 to 3 mm long on the lower part. The leaf sheaths are purple-pigmented, glaucous, and glabrous on the outer surfaces, and are beset with hairs on one of the lateral edges. The auricles are 1.5 to 2 mm long with several hairs 5 mm or less in length. The ligules project 3 to 4 mm from the point of attachment to the leaf.

The spikes are extremely fragile, 8 to 10 mm wide across the two-ranked face, 10 to 12 cm long exclusive of the awns, and are composed of from thirty to sixty 3- to 5-flowered sterile spikelets (fig. 3, *B*). At maturity the rachis breaks with a clean fracture at its joints into small segments, at the apex of each of which is attached a spikelet (pl. 10, *B*; pl. 7, *B*; pl. 8, *B*).

The spikelets are 6 to 8 mm wide and 15 to 18 mm long exclusive of the awns (pl. 10, *B*). On the exterior side and center of the spikelet at the base is a prominent tuft of bristles which are 3 mm or less in length and which extend to the fringed edges of the rachis internode to which the spikelet is attached (pl. 6, *B*). At the base

of the spikelet on the side facing the rachis is a smaller tuft of bristles which are 1 mm or less in length (pl. 7, *B*).

The rachis internodes are 3 mm long, intermediate in shape between those of the two parents, glabrous on the convex and concave surfaces, and the edges are fringed with numerous bristles 5 mm or less in length (pl. 8, *B*).

The glumes are 2 mm wide, 10 to 12 mm long exclusive of the awns, glabrous, glaucous, white streaked with black pigment, papillate usually only on the prominent nerves, and each possesses five nerves, the two more prominent of which form keels. The rear one of the most prominent nerves is the stronger and forms the primary keel, which terminates in a black scabrid awn 35 to 38 mm long. The prominent nerve in the front forms a secondary keel and is scabrid. The primary keel is beset throughout its entire length with untufted superasperites 2.8 mm or less in length. These superasperites were present on the specimen illustrated in plate 10, *B*, but because of the laterally compressed spikelets they are completely obscured. Between the two prominent nerves is a longitudinal channel through which passes a conspicuous scabrid nerve which unites with a primary keel at the apex of the glume. The glume shoulders are intermediate in width between those of the parents, slightly elevated, and nondentate (pl. 10, *B*).

The lemmas are 2 mm wide, 12 to 14 mm long, papillate, slightly scabrous at their upper exposed surfaces, and possess nine inconspicuous nerves, the central one of which is partly keeled and terminates in a black scabrid awn 7 to 9 cm long. At the apex of the lemma are several superasperites 1 to 2 mm long (pl. 10, *B*).

The paleas are entire, not split. The lodicules are 0.9 mm wide and 1.8 mm long and are beset with hairs 0.65 mm long.

TRITICUM DICOCCUM × HAYNALDIA VILLOSA

The plants of the hybrid *Triticum dicoccum* × *Haynaldia villosa* have an upright habit of growth and attain an average height at maturity of 196.8 cm. The culms are hollow immediately below the head, glaucous, and slightly purple-pigmented. The nodes are very glaucous and puberulent.

The leaf blades are 8 to 10 mm wide and possess hairs on the upper and lower surfaces 1 to 1.5 mm long. The edges of the leaf blades are scabrid, and the lower edges of the blades are beset with hairs 0.5 to 1 mm long. The leaf sheaths are weakly glaucous, glabrous, and purple-streaked. The lateral edges of the sheaths are glabrous. The auricles are 2 mm long with a few hairs 3 mm or less in length. The ligules project 2 mm from the point of attachment to the leaves.

The spikes are very fragile, somewhat laterally compressed, 8 to 10 mm wide, 8 to 10 cm long exclusive of the awns and consist of from twenty to twenty-five 2- or 3-flowered sterile spikelets (fig. 4, *B*). At maturity the rachis breaks with a clean fracture at its joints into small segments at the apex of each of which is attached a spikelet (pl. 5, *E*).

The spikelets are 4.5 to 5.5 mm wide and 12 to 13 mm long exclusive of the awns (pl. 5, *E*). On the exterior side of the spikelet at the base is a distinct tuft of bristles which are 1 mm or less in length

(pl. 5, *E*). At the base of the spikelet on the side facing the rachis is also a tuft of hairs which are less than 0.5 mm long.

The rachis internodes are 4 to 5 mm long, nonglaucous, and glabrous except on the two lateral edges, which are fringed with numerous bristles 1 to 2 mm long (pl. 5, *E*).

The glumes are slightly glaucous, 4 mm wide, 11 to 12 mm long exclusive of the awns, papillate usually in greater abundance on the nerves, and possess 5 to 6 nerves, 2 or 3 of which may be scabrid. The two most prominent nerves form keels. The primary keel faces the rachis, possesses asperites on the lower edge and superasperites 1.5 mm or less in length on the upper edge, and terminates in an awn or beak 0.5 to 3.3 cm long (pl. 5, *E*). Between the prominent nerves is a longitudinal, shallow channel through which passes laterally 1 to 3 prominent nerves. The glume shoulders are intermediate in width between those of the parents and have a sharp-pointed tooth (pl. 5, *E*).

The lemmas are 3 mm wide, 12 to 13 mm long exclusive of the awns, papillate, slightly scabrid at the apex, and possess 7 to 8 nerves, the middle one of which forms an imperfect keel that terminates in a slightly purple-pigmented scabrid awn 8 to 8.7 cm long. The exposed portion of the keel at the apex of the lemma is usually beset with superasperites 0.8 to 1.0 mm long (pl. 5, *E*).

The paleas are entire, not split. The lodicules are 1 mm wide and 2 mm long and are beset with hairs 0.4 mm long.

TRITICUM DURUM × HAYNALDIA VILLOSA

The plants of the hybrid *Triticum durum* × *Haynaldia villosa* have an upright habit of growth and attain an average height at maturity of 152.4 cm. The culms are glaucous, purple-pigmented, and hollow at a point 2.5 cm below the head (pl. 3, *E*). The nodes are glaucous and glabrous.

The leaf blades are 10 to 11 mm wide and covered on the upper and lower surfaces with hairs 1 to 1.25 mm long. Hairs 1 to 1.25 mm long are present also on the edges of the leaves for a distance of 6 to 7 cm upward from the base. The edges of the leaf blades are scabrid. The leaf sheaths are glaucous, glabrous, and purple-pigmented and are devoid of hairs on the lateral edge. The auricles are 2.5 to 3 mm long and possess hairs 4 mm or less in length. The ligules project 3 mm from the point of attachment to the leaf.

The spikes are extremely fragile, 10 to 12 mm wide across the two-ranked face, 8 to 12 cm long, and composed of from twenty to thirty 3- or 4-flowered sterile spikelets (fig. 5, *B*). At maturity the rachis breaks with a clean fracture at its joints into small segments, at the apex of each of which is attached a spikelet (pl. 11, *E*).

The spikelets are 7 to 9 mm wide and 12 to 14 mm long exclusive of the awns (pl. 11, *E*). On the exterior side of the spikelet at the base is a collar of bristles, the longest of which do not exceed 1.5 mm (pl. 11, *E*). At the base of the spikelet on the side facing the rachis is a tuft of slender bristles 0.4 mm or less in length.

The rachis internodes are 4 mm long, glaucous, and glabrous, and the edges are fringed with numerous bristles, the longest of which does not exceed 2 mm (pl. 11, *E*).

The glumes are papillate, glaucous, 2 mm wide, 9 to 10 mm long exclusive of the awns, and possess four prominent nerves, the most conspicuous of which forms the keel and terminates in a beak or short awn 10 to 26 mm long. The keel has short asperites except near the apex, where they take the shape of long bristlelike structures about 1 mm long. The glume shoulders are intermediate in width between those of the parents, elevated, and nondentate (pl. 11, *E*).

The lemma is papillate, glaucous, slightly asperous at its upper exposed surface, 2.5 mm wide and 11 to 12 mm long, and possesses 9 to 10 nerves, the most prominent of which terminates in a slightly purple-pigmented scabrous awn 3 to 7 cm long. At the apex of the lemma on the keel are usually several conspicuous trichomes 1 mm or less in length (pl. 11, *E*).

The paleas are entire, not split. The lodicules are 1 mm wide and 1.8 mm long and are beset with hairs 0.3 mm long.

TRITICUM POLONICUM × HAYNALDIA VILLOSA

The plants of the hybrid *Triticum polonicum* × *Haynaldia villosa* have an upright habit of growth and attain an average height at maturity of 133.3 cm. The culms are glaucous, hollow, and purple-pigmented. The nodes are usually glabrous, though rarely they are sparsely puberulent and slightly glaucous.

The leaf blades are 10 to 12 mm wide and are beset on the upper and lower surfaces with a few hairs 0.5 to 1 mm long. The margins of the leaf blades are scabrid and beset with hairs 2 mm or less in length for a distance of several centimeters from the base of the leaf. The leaf sheaths are usually glaucous, streaked with purple pigment, and glabrous on the surfaces and edges. Sometimes on the lower leaf sheaths one lateral edge may be abundantly covered with hairs 1.5 to 2 mm long. The auricles are 2 to 3 mm long, with many hairs 5 mm or less in length. The ligules project 2.5 to 3 mm from the point of attachment to the leaf.

The spikes are fragile, 10 to 12 mm wide across the two-ranked face, 12 to 14 cm long exclusive of the awns, and consist of from twenty-five to thirty 2- to 5-flowered sterile spikelets (fig. 6, *B*).

The spikelets are 9 to 13 mm wide and 18 to 20 mm long exclusive of awns (pl. 9, *B*). On the exterior side of the spikelet at the base is a prominent tuft of bristles which are 0.5 to 2 mm long (pl. 9, *B*). At the base of the spikelet on the side facing the rachis is a tuft of bristles, which are 0.5 mm or less in length and extend to the right and left, joining the lateral fringes of bristles on the edges of the rachis internode to which the spikelet is attached.

The rachis internodes are 5 to 6 mm long, glaucous, and glabrous except on their lateral edges, which may be entirely fringed with bristles 0.5 to 2.5 mm long, the shorter bristles being at or near the base and increasing progressively as they approach the apex. Sometimes the lower edge of the rachis internode for a distance of 1 or 2 mm may be entirely devoid of bristles (pl. 9, *B*).

The glumes are partly glaucous, papillate, 3 mm wide, 17 to 19 mm long exclusive of the awns, and possess 9 to 10 nerves, the most prominent of which forms a sharp scabrid keel that terminates in a scabrid awn 2 to 3 cm long (pl. 9, *B*). The keel throughout its entire length

is beset with asperites. Besides the keel 1 or 2 other prominent nerves may be scabrid. The apex and membranous portion of the glume are abundantly puberulent or pubescent (pl. 9, *B*). No superasperites appear on the keel. The glume shoulders are intermediate in width between those of the parents, elevated, and nondentate (pl. 9, *B*).

The lemmas are 3 to 3.5 mm wide, 17 to 19 mm long exclusive of awns, papillate, puberulent, and pubescent on the edges and upper exposed portions (pl. 9, *B*). The lemmas also have 8 to 9 nerves, the middle one of which forms a partial keel that is beset with a few short superasperites and terminates in a purplish-black scabrid awn 2 to 6.5 cm long (pl. 9, *B*). Some of the nerves on the exposed portion of the lemmas may be scabrid also.

The paleas are entire, not split. The lodicules are 1 mm wide, 2.3 mm long and are beset with hairs 0.58 mm long.

TRITICUM TURGIDUM × HAYNALDIA VILLOSA

The plants of the hybrid *Triticum turgidum* × *Haynaldia villosa* have an upright habit of growth and attain an average height at maturity of 177.8 cm. Each culm is hollow with a small cavity at a point 2.5 cm below the head, glaucous, and purple-pigmented. The nodes are glabrous.

The leaf blades are 7 to 9 mm wide and puberulent on both the upper and lower surfaces. The edges of the blades are scabrid and possess a few hairs 1 to 2 mm long on the lower part of the blades. The auricles are 2 mm long with a few hairs 3 mm or less in length. The leaf sheaths are purple-pigmented, glabrous, slightly glaucous on the surfaces, and glabrous on the overlapping edges. The ligules project 3 to 4 mm from the point of attachment to the leaf.

The spikes may be simple or branched, very fragile, 9 to 40 mm wide across the two-ranked face, 12 to 13 cm long exclusive of the awns, and consist of from forty to sixty-five 2- to 4-flowered spikelets (fig. 7, *B*).

The spikelets are 8 to 9 mm wide and 17 to 18 mm long exclusive of the awns (pl. 11, *B*). Most of the spikelets are completely sterile, although a few kernels were obtained that are longer than either of the parents (pl. 2, *F*). On the exterior side of the spikelet at the base is a tuft of bristles which are 2.5 or less in length and extend to the two lateral edges of the rachis internode to which the spikelet is attached (pl. 11, *B*). At the base of the spikelet on the side facing the rachis is another tuft of bristles which are 1 mm or less in length.

The rachis internodes are intermediate in shape between those of the parents, 3 to 3.5 mm long, and glabrous on the surfaces, and on each of the two lateral edges is a fringe of bristles 0.5 to 3.5 mm long, the longest being located at the apex of the rachis internode and the shortest at the base (pl. 11, *B*).

The glumes are 4 mm wide, 7 to 9 mm long exclusive of the awns, papillate on the exterior surface except on the membranous portion near the edges, and each possesses four nerves, the two most prominent of which form keels. The rear one of the two most prominent nerves is the stronger and forms the primary keel, at the apex of which is a black awn 1.5 to 2.5 cm long (pl. 11, *B*). The glume

shoulders are intermediate in width between those of the parents, elevated, and nondentate (pl. 11, *B*).

The prominent nerve nearest the front forms a secondary keel. The two keels of the glumes of this hybrid are beset with untufted superasperites which have a maximum length of 8.3 mm (pl. 11, *B;* pl. 12, *B*). Between the two prominent nerves is a shallow, longitudinal channel through which passes a conspicuous nerve which unites with the primary keel at the apex of the glume.

The lemmas are 3 to 4 mm wide and 10 to 13 mm long, papillate, and terminate in a purplish black scabrid awn 5 to 9 cm long. At the apex of the lemma on the keel are several untufted superasperites 1.7 mm or less in length (pl. 1, *E;* pl. 11, *B;* and pl. 12, *E*). Also a few asperites may be found on the exposed portion of the lemma, usually on the nerves.

The paleas are entire, not split. The lodicules are 0.9 mm wide and 1.8 mm long and are beset with hairs 0.5 mm long.

SECALE FRAGILE × HAYNALDIA VILLOSA

The plants of the hybrid *Secale fragile* × *Haynaldia villosa* have an upright habit of growth and attain an average height at maturity of 106.7 cm. The culms are hollow, purple-pigmented, and glaucous, and the peduncle below the head for several centimeters is covered with hairs which are less than 1 mm in length (pl. 2, *B;* pl. 3, *H*). The nodes are glabrous.

The leaf blades are 5 to 6 mm wide and possess on the upper and lower surfaces an abundance of hairs 1 to 2 mm long. The edges of the leaf blades are scabrid and beset with hairs 1 to 3.0 mm long. Just above the ligule on the leaf is a collar of hairs slightly shorter and fewer in number than those of the *Secale* parent (pl. 4, *B*). The exterior surfaces of the lower leaf sheaths are hairy or puberulent on the exterior surfaces and glabrous on the edges. The leaf sheaths are also weakly glaucous, and slightly purple-pigmented, and the overlapping lateral edges are devoid of hairs. The auricles are 2 mm long with several hairs 4 mm or less in length. The ligules project 3 mm from the point of attachment to the leaves.

The spikes are extremely fragile, 8 to 9 mm wide across the two-ranked face, 10 to 12 cm long exclusive of the awns, and consist of from thirty to thirty-eight 3- or 4-flowered sterile spikelets (fig. 8, *B*). At maturity the rachis breaks with a clean fracture at its joints into small segments, at the apex of each of which is attached a spikelet (pl. 10, *E*).

The spikelets are 5 to 7 mm wide and 16 to 18 mm long exclusive of the awns (pl. 10, *E*). On the exterior side of the spikelet at the base is a tuft of short bristles 0.35 mm or less in length (pl. 10, *E*). At the base of the spikelet on the side facing the rachis is a tuft of short bristles which are 0.5 mm or less in length.

The rachis internodes are 3 mm long and usually glabrous on the exterior surface, though occasionally there may be an irregular distribution of extremely short bristles (pl. 10, *E*). The edges of the rachis internodes are fringed with numerous bristles 3.5 mm or less in length.

The glumes are slightly glaucous, 1 mm wide, 8 to 10 mm long exclusive of the awns, papillate except on the membranous portions

near the edges, and possess two prominent scabrid nerves which form keels and are separated by a boat-shaped depression about 0.75 mm wide at the center. The two keels converge at the base and apex. At the apex of each glume is a long scabrous awn 3 to 5.5 cm long (pl. 10, *E*). The primary or more prominent keel, however, possesses abundant superasperites 1.9 mm or less in length, while the secondary keel usually is beset with asperites. The glume shoulders are intermediate in width between those of the parents, slightly elevated to oblique, and nondentate (pl. 10, *E*).

The lemmas are 2.5 mm wide, 12 to 14 mm long exclusive of the awns, and papillate on the exterior surface, and each has five nerves, the middle one of which is keeled and terminates in a purple, scabrid awn 5 to 7 cm long (pl. 10, *E*). The keels of the lemmas throughout their entire length are beset with slender superasperites 1.4 mm or less in length. The exposed surface of the lemma and the margins usually are beset with reduced spur asperites (pl. 10, *E*). The edges of the lemma are beset with thin hairs 0.75 mm or less in length.

The paleas are entire, not split. The lodicules are 1 mm wide and 2.9 mm long and are beset with hairs 0.66 mm long.

DISCUSSION

Hybrid seeds were obtained and the F_1 plants matured from the crosses of *Haynaldia villosa* on *Triticum aegilopoides*, *T. timopheevi*, *T. dicoccoides*, *T. dicoccum*, *T. durum*, *T. turgidum*, *T. polonicum*, and *Secale fragile*. Attempts to cross *T. vulgare*, *T. spelta*, *T. compactum*, and *S. cereale* with *H. villosa* have met with failure. Several varieties of *T. vulgare* when pollinated with pollen from *H. villosa* produced enlarged structures which were devoid either of embryos or of endosperms. One hybrid seed of the cross *T. vulgare* var. C. I. 6223 × *H. villosa* germinated but died before the formation of the third leaf.

From Strampelli's successful cross of *T. vulgare* with *T. villosum* (*Haynaldia*), as reported by Raineri (*6*), and a similar cross with another, *T. spelta* × *T. villosum*, by Tschermak (*8*, *9*), it is probable that these investigators may have had a variety of *H. villosa* different from that used by the writer. The writer has been unable to cross *T. vulgare* and *T. spelta* with *H. villosa*.

The form of *Haynaldia villosa* used by the writer was procured from Russia, grew normally to a height of 120 to 130 cm in a greenhouse, and set seed satisfactorily under these conditions and out of doors. Another form of *H. villosa* introduced from Denmark under the name *Agropyron villosum* grew to a height of only 40 cm and showed abnormal anther dehiscence, which resulted in almost complete sterility of the plants. Because of the difficulty in procuring pollen from the latter form no attempts were made to make hybrids with it.

Special attention was devoted to a study of the trichomes because of the variation of their shape, length, and thickness.

The lodicule is an interesting organ which has received little attention in morphological studies of the grasses. Preliminary studies of the lodicules of *Triticum*, *Secale*, *Aegilops*, *Haynaldia*, and *Agropyron* species indicate that these organs have certain characteristics that may be used in the identification of species and

genera. There are differences in shape, dimensions, and marginal indentations, and in the length and distribution of the hairs on the exterior surfaces. Plate 13 shows the lodicules of *T. aegilopoides*, *T. polonicum*, *S. fragile*, and *H. villosa* and of F_1 hybrids of the first three species with *Haynaldia*.

The various species used in the production of the hybrids described fall into two chromosome groups. *Triticum aegilopoides*, *Secale fragile*, and *Haynaldia villosa* are diploid species, while *T. timopheevi*, *T. dicoccoides*, *T. dicoccum*, *T. polonicum*, *T. durum*, and *T. turgidum* are tetraploid species. Although *H. villosa*, *S. fragile*, and *T. aegilopoides* each have seven haploid chromosomes, when H. *villosa* was crossed with *S. fragile* and *T. aegilopoides* the F_1 hybrids were completely self-sterile. This has particular significance, especially in view of the fact that in the latter hybrid a maximum of five pairs of chromosomes were observed during meiosis. With the exception of *T. turgidum* var. Alaska, all of the tetraploid species referred to above when crossed with *H. villosa*, a diploid species, produced hybrids that were completely self-sterile. The cross *T. turgidum* var. Alaska × *H. villosa* is the only F_1 hybrid among all of the crosses made that showed any fertility, and this produced only an average seed set of 3.8 percent with a maximum seed set of 11.1 percent for a single plant. The F_2 plants of this cross produced an average seed set of 29.7 percent with a maximum seed set of 58.8 percent for a single plant, and the F_3 plants produced an average seed set of 58.5 percent with a maximum seed set of 76.9 percent for a single plant. No apparent segregation occurred in the F_2 and subsequent generations of the cross *T. turgidum* × *H. villosa*, the F_1 type remaining fixed in its morphological characters. In figure 9 are shown F_2 spikes.

In general, the F_1 hybrids of the above crosses resemble the *Triticum* or *Secale* parent, although a critical study indicates that the majority of the characters of the F_1 hybrids are intermediate between those of the parents involved. Some characters of the F_1, however, show a decided increase over those of either parent, while others show a dominance of one or the other parent. For convenience in comparison 52 characters showing characteristics of the parents and F_1 hybrids are listed in table 2. These are discussed in the following paragraphs, which are numbered to correspond with the table.

1. The F_1 hybrids of *Triticum timopheevi*, *T. dicoccoides*, *T. dicoccum*, *T. durum*, *T. turgidum*, and *T. polonicum* with *Haynaldia villosa* are greater in stature than either parent, while those of *T. aegilopoides* and *Secale fragile* with *H. villosa* are somewhat intermediate to parental stature.

2. The culms of *Haynaldia villosa* are hollow at a point 2.5 cm below the head and possess large cavities. *Triticum polonicum* and *Secale fragile* have hollow culms with small cavities. When these are crossed with *H. villosa* the F_1 plants have cavities intermediate between those of the parents. *T. aegilopoides*, *T. dicoccoides*, *T. dicoccum*, and *T. turgidum* all have solid culms at a point 2.5 cm below the head. When these are crossed with *H. villosa* the F_1 hybrids have culms with cavities similar in size to those of the *Haynaldia* parent. Crosses between *T. timopheevi* and *H. villosa*, both of which have large culm cavities, produced F_1 hybrids with culm cavities larger than those of either parent. Crosses between *T. durum* and *H. villosa*, with culm cavities similar in size, produced F_1 plants with culm cavities not appreciably different in size from those of either parent. Cross sections of the culms 2.5 cm below the spike of the parents and F_1 hybrids of the crosses *T. aegilopoides*, *T. durum*, and *S. fragile* with *H. villosa* are shown in plate 3.

FIGURE 9.—F_2 spikes of *Triticum turgidum* × *Haynaldia villosa*: *A*, Simple; *B*, ramified. Natural size.

TABLE 2.—*Some characters of seven species of Triticum, Secale fragile, and Haynaldia villosa and their expression in the F1 hybrids resulting from the crossing of Triticum and Secale species with H. villosa.*

[Plus (+) denotes presence, and minus (−) absence, of character [1] named]

Characters [2]	*Haynaldia villosa* male parent	*T. aegilopoides* × *H. villosa*		*T. timopheevi* × *H. villosa*		*T. dicoccoides* × *H. villosa*		*T. dicoccum* × *H. villosa*	
		Triticum parent	F_1 hybrid	*Triticum* parent	F_1 hybrid	*Triticum* parent	F_1 hybrid	*Triticum* parent	F_1 hybrid
1. Stature of plant (average)—cm	124.5	93	116.8	142.2	149.9	76.2	154.9	68.6	196.8.
2. Solidity of culm 1 inch below head	Hollow	Solid	Hollow	Hollow	Hollow	Solid	Hollow	Solid	Hollow.
3. Anthocyanin in culm	(+)	(+)	(+)	(−)	(+)	(+)	(+)	(−)	(+) (int.).
4. Pubescence of culm	(−)		(−)	(−)	(−)	(−)	(−)	(−)	(−).
5. Glaucousness of culm	(+)		(+) (int.)	(+)	(+)	(+)	(+)	(−)	(+) (int.).
6. Pubescence of culm nodes	(−)	(+)	(+) (int.)	(+)	(+) (int.)	(+)	(+) (int.)	(+)	(+) (int.).
7. Width of leaf blades (average)—mm	7	5	6.5	8	9.5	7	7.5	11	9.
8. Pubescence of leaf-blade margins	(+)	(+)	(+)	(+)	(+)	(−)	(+)	(−)	(+).
9. Scabrousness of leaf-blade margins	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+).
10. Pubescence of leaf sheaths	(−)	(+)	(+)	(+)	(+)	(−)	(−)	(−)	(−).
11. Glaucousness of leaf sheaths	(+)	(−)	(+)	(+)	(+)	(−)	(+)	(+) (weak)	(+) (weak).
12. Anthocyanin in leaf sheaths	(+)	(−)	(+)	(−)	(+)	(+)	(+)	(−)	(+).
13. Pubescence of leaf-sheath margins	(−)	(+)	(+)	(+)	(+)	(+)	(+)	(−)	(−).
14. Length of auricles (maximum)—mm	2	1	1.5	1	1.2	1	2	2	2
15. Length of hairs on auricles (maximum)—do	4	5	3	5	6	1.5	5	0.7	3.
16. Length of ligules (maximum)—do	3	1	1.5	1	1.3	3	4	2	2.
17. Width of spike (average)—do	12	5	7	13.5	11	8.5	9	9	9.
18. Length of spike (average)—cm	8	8	11	7	10.2	8	11	8	9.
19. Spikelets—number	20-32 (26)	20-40 (30)	30-46 (38)	18-21 (19)	30-35 (33)	16-18 (17)	30-60 (45)	16-24 (20)	20-25 (23).
20. Width of spikelets (average)—mm	5.5	2.7	7	7.5	4.8	4.5	7	6.5	5
21. Length of spikelets (average)—do	13.5	9	10	17	17.5	16	16.5	11	12.5.
22. Branching of rachis	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple.
23. Fragility of rachis	Very fragile.	Very fragile.	Very fragile.	Nonfragile.	Very fragile.	Very fragile.	Very fragile.	Fragile	Very fragile.
24. Shape of rachis internodes	Obovate	Oblong	Intermediate.	Blunt-cuneate.	Intermediate.	Oblong	Intermediate.	Oblong	Intermediate.
25. Length of rachis internodes—mm	2.5	2.7	2.7	2	3.3	4	3	3	4.5.
26. Arrangement of bristles on rachis	Tufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted.
27. Width of glumes (average)—mm	2	1	1.8	2.5	2.3	2	2	2.5	4.
28. Length of glumes (average)—do	5.5	6	7.5	9	8	12.5	11	9.5	11.5.
29. Length of beak on glumes (maximum)—do	30	1.5	25	5	50	2	38	0.5	33.
30. Shape of shoulder on glumes	Elevated-rounded.	Apiculate	Apiculate-oblique (int.).	Apiculate	Apiculate (int.).	Apiculate	Rounded (int.).	Acute to apiculate.	Rounded (int.).
31. Size of papillae on glumes	Large	Small	Medium	(−)	Medium	Small	Medium	Small	Medium.
32. Canaliculation of glumes	(+)	(−)	(+) (int.)	(−)	(+) (int.)	(−)	(+) (int.)	(−)	(+) (int.).
33. Carination of glumes	Bicarinate	Unicarinate.	Bicarinate (int.).	Unicarinate.	Bicarinate (int.).	Unicarinate.	Bicarinate (int.).	Unicarinate.	Bicarinate (int.).
34. Glaucousness of glumes	(+)	(−)	(+)	(+)	(+)	(−)	(+)	(−)	(+).
35. Pubescence of glumes	(−)	(−)	(−)	(+) (heavy)	(+) (weak)	(−)	(−)	(−)	(−).
36. Width of glumes (average)—mm	3	1.7	2	3.3	2.7	2	2	3.	3.

35. Pubescence of glumes	(−)	(−)	(−)	(+) (heavy)	(+) (weak)	(−)	(−)	(−)	(−).
36. Width of lemma (average)—mm.	2	1.7	2	3.3	2.7	2	2	3	3.
37. Length of lemma (average)—mm.	12	8	10.5	13.5	13	14.5	13	10.5	12.5.
38. Length of awn on lemma (maximum)—mm.	4.5	9	6.5	11	4.7	17.5	9	9	8.7.
39. Pigment in awn on lemma	Purple	Yellow	Weak purple.	Black	Purplish black.	Black	Black	Yellow	Weak purple.
40. Size of papillae on lemma	Large	Small	Medium	Small	Medium	Small	Medium	Small	Medium.
41. Length of trichomes on glume keels	Long	Short	Intermediate.	Short	Intermediate.	Short	Intermediate.	Short	Intermediate.
42. Arrangement of trichomes on glume keels	Tufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted.
43. Length of trichomes on lemma keels	Long	Short	Intermediate.	Short	Intermediate.	Short	Intermediate.	Short	Intermediate.
44. Arrangement of trichomes on lemma keels	Tufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted.
45. Length of bristles at base of spikelet on exterior side (maximum), mm.	0.5	3	2	2	1	5	3	1.25	1.
46. Bristles at base of spikelet on exterior side, number.	Few	Many	Intermediate.	Many	Intermediate.	Many	Intermediate.	Many	Intermediate.
47. Length of bristles at base of spikelet on side facing rachis (maximum), mm.	0.3	0.5	0.5	1	0.35	1.5	1	0.5	0.5.
48. Bristles at base of spikelet on side facing rachis, number.	Few	Many	Intermediate.	Many	Intermediate.	Many	Intermediate.	Many	Intermediate.
49. Width of lodicules (maximum)—mm.	0.9	0.33	0.5	0.6	0.8	0.9	0.9	0.9	1.
50. Length of lodicules (maximum)—mm.	2	0.8	1.5	1.8	1.9	1.6	1.8	1.7	2.
51. Length of hairs on lodicules (maximum), mm.	0.05	0.33	0.42	0.65	0.3	0.6	0.65	0.6	0.4.
52. Self-fertility of plant	Fully fertile.	Fully fertile.	Infertile.	Fully fertile.	Infertile.	Fully fertile.	Infertile.	Fully fertile.	Infertile.

[1] Int.=intermediate.
[2] Average and maximum denote, respectively, average and maximum of several measurements.

TABLE 2.—*Some characters of seven species of Triticum, Secale fragile, and Haynaldia villosa and their expression in the F_1 hybrids resulting from the crossing of Triticum and Secale species with H. villosa*—Continued

[Plus (+) denotes presence, and minus (−) absence, of character [1] named]

Characters [2]	*Haynaldia villosa* male parent	*T. durum* × *H. villosa*		*T. polonicum* × *H. villosa*		*T. turgidum* × *H. villosa*		*S. fragile* × *H. villosa*	
		Triticum parent	F_1 hybrid	*Triticum* parent	F_1 hybrid	*Triticum* parent	F_1 hybrid	*Secale* parent	F_1 hybrid
1. Stature of plant (average)—cm	124.5	132	152.4	124.5	133.3	127	177.8	76	106.7.
2. Solidity of culm 1 inch below head	Hollow	Hollow	Hollow	Small cavity.	Hollow (int.).	Solid	Hollow	Hollow	Hollow.
3. Anthocyanin in culm	(+)	(−)	(+)	(−)	(+) (int.)	(−)	(+) (int.)	(+)	(+).
4. Pubescence of culm	(−)	(−)	(−)	(−)	(−)	(−)	(−)	(+)	(+).
5. Glaucousness of culm	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+) (weak)	(+).
6. Pubescence of culm nodes	(−)	(−)	(−)	(+)	(+) (int.)	(−)	(−)	(+)	(−).
7. Width of leaf blades (average)—mm	7	9	10.5	20	11	16.5	8	6.5	5.5.
8. Pubescence of leaf-blade margins	(+)	(−)	(+)	(+)	(+)	(−)	(+)	(+)	(+).
9. Scabrousness of leaf-blade margins	(+)	(+)	(+)	(+)	(+)	(−)	(+)	(+)	(+).
10. Pubescence of leaf sheaths	(−)	(−)	(−)	(−)	(+)	(−)	(−)	(+)	(+).
11. Glaucousness of leaf sheaths	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+) (weak).
12. Anthocyanin in leaf sheaths	(+)	(−)	(+)	(−)	(+)	(−)	(+)	(+)	(+).
13. Pubescence of leaf-sheath margins	(−)	(−)	(−)	(−)	(−)	(−)	(−)	(−)	(−).
14. Length of auricles (maximum)—mm	2	2	3	1.5	3	3	2	0.5	2.
15. Length of hairs on auricles (maximum)—do	4	(−)	4	(−)	5	0.25	3	0.4	4.
16. Length of ligules (maximum)—do	3	2.5	3	2	3	3	4	0.7	3.
17. Width of spike (average)—do	12	7.5	11	13	11	23	23	7.5	8.5.
18. Length of spike (average)—cm	8	7.5	10	12	13	10	12	9.5	11.
19. Spikelets—number	20-32 (26)	18-24 (21)	20-30 (25)	18-22 (20)	25-30 (27)	30-80 (55)	40-65 (47)	26-36 (31)	30-38 (34).
20. Width of spikelets (average)—mm	5.5	11	8	11	11	7.5	8.5	5	6.
21. Length of spikelets (average)—do	13.5	12.5	13	22.5	19	9.5	17.5	15	17.
22. Branching of rachis	Simple	Simple	Simple	Simple	Simple	Branched	Branched	Simple	Simple.
23. Fragility of rachis	Very fragile.	Nonfragile	Very fragile.	Nonfragile	Fragile	Nonfragile	Very fragile.	Very fragile.	Very fragile.
24. Shape of rachis internodes	Obovate	Oblong	Intermediate.	Oblong	Intermediate.	Oblong	Intermediate.	Oblong	Intermediate.
25. Length of rachis internodes—mm	2.5	4	4	8	6	2.8	3.3	4	3.
26. Arrangement of bristles on rachis	Tufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted	Nontufted.
27. Width of glumes (average)—mm	2	1.7	2	3	3	2.5	4	0.5	1.
28. Length of glumes (average)—do	5.5	7.5	9.5	22	18	5.5	8	13.5	9.
29. Length of beak on glumes (maximum)—do	30	2	26	5	30	0.5	25	60	55.
30. Shape of shoulder on glumes	Elevated-rounded.	Oblique	Elevated (int.).	Apiculate	Rounded (int.).	Oblique	Rounded (int.).	(−)	Acute-rounded (int.).
31. Size of papillae on glumes	Large	Small	Medium	Small	Medium	Small	Medium	Small	Medium.
32. Canaliculation of glumes	(+)	(−)	(+) (int.)	(−)	(+) (int.)	(−)	(+) (int.)	(−)	(+).
33. Carination of glumes	Bicarinate	Unicarinate.	Bicarinate (int.).	Unicarinate.	Bicarinate (int.).	Unicarinate.	Bicarinate (int.).	Unicarinate.	Bicarinate (int.).
34. Glaucousness of glumes	(+)	(+)	(+)	(+)	(+)	(+)	(+)	(+) (weak)	(+).
35. Pubescence of glumes	(−)	(−)	(−)	(+)	(+) (int.)	(−)	(−)	(−)	(−).
36. Width of lemma (average)—mm	2	2.2	2.5	4	3.3	3	3.5	2.5	2.5.
37. Length of lemma (average)—mm	12	8.5	11.5	24	18	8	11.5	16	13.
38. Length of awn on lemma (maximum)—mm	4.5	16	7	12	6.5	11	9	12	7.

37. Length of lemma (average)..... mm..	12.....	8.5.....	11.5.....	24.....	18.....	8.....	11.5.....	16.....	13.
38. Length of awn on lemma (maximum) mm..	4.5.....	16.....	7.....	12.....	6.5.....	11.....	9.....	12.....	7.
39. Pigment in awn on lemma.....	Purple.....	Yellow.....	Weak purple.	Black.....	Purplish black.	Black.....	Purplish black.	Purple.....	Purple.
40. Size of papillae on lemma.....	Large.....	Small.....	Medium.....	Small.....	Medium.....	Small.....	Medium.....	Small.....	Medium.
41. Length of trichomes on glume keels.....	Long.....	Short.....	Intermediate.	Short.....	Intermediate.	Short.....	Intermediate.	Short.....	Intermediate.
42. Arrangement of trichomes on glume keels...	Tufted.....	Nontufted..	Nontufted..	Nontufted..	Nontufted..	Nontufted..	Nontufted..	Nontufted..	Nontufted.
43. Length of trichomes on lemma keels.....	Long.....	Short.....	Intermediate.	Short.....	Intermediate.	Short.....	Intermediate.	Short.....	Intermediate.
44. Arrangement of trichomes on lemma keels..	Tufted.....	Nontufted..	Nontufted..	Nontufted..	Nontufted..	Nontufted..	Nontufted..	Nontufted..	Nontufted.
45. Length of bristles at base of spikelet on exterior side (maximum), mm.	0.5.....	2.....	1.5.....	2.5.....	2.....	2.....	1.....	0.2.....	0.35.
46. Bristles at base of spikelet on exterior side, number.	Few.....	Many.....	Intermediate.	Many.....	Intermediate.	Many.....	Intermediate.	Several.....	Intermediate.
47. Length of bristles at base of spikelet on side facing rachis (maximum), mm.	0.3.....	0.35.....	0.55.....	0.3.....	0.5.....	0.5.....	0.5.....	0.35.....	0.5.
48. Bristles at base of spikelet on side facing rachis, number.	Few.....	Many.....	Intermediate.	Many.....	Intermediate.	Many.....	Intermediate.	Many.....	Intermediate.
49. Width of lodicules (maximum)..... mm..	0.9.....	0.9.....	1.....	1.0.....	1.0.....	0.7.....	0.9.....	1.1.....	1.
50. Length of lodicules (maximum)..... mm..	2.....	1.3.....	1.8.....	1.6.....	2.3.....	1.1.....	1.8.....	2.9.....	2.9.
51. Length of hairs on lodicules (maximum), mm.	0.05.....	0.5.....	0.3.....	1.35.....	0.38.....	0.7.....	0.5.....	1.25.....	0.66.
52. Self-fertility of plant.....	Fully fertile.	Fully fertile.	Infertile.....	Fully fertile.	Infertile.....	Fully fertile.	Weakly fertile.	Fully fertile.	Infertile.

[1] Int.=intermediate.
[2] Average and maximum denote, respectively, average and maximum of several measurements.

81210—35——3

3. Anthocyanin formation in the stems is dominant over the absence of this function. The culms of *Triticum aegilopoides*, *T. dicoccoides*, and *Secale fragile* possess anthocyanin pigment. *T. timopheevi* *T. dicoccum*, *T. polonicum*, *T. durum*, and *T. turgidum* have culms devoid of anthocyanin pigment. When these latter are crossed with *Haynaldia villosa*, which has anthocyanin pigment in its stems, the F_1 hybrid plants possess anthocyanin pigment.

4. Papillate and pubescent peduncles are dominant over glabrous peduncles. All of the species here reported on, with the exception of *Secale fragile* and *Triticum timopheevi*, have glabrous peduncles. *T. timopheevi* has papillate peduncles and when crossed with *Haynaldia villosa* with glabrous peduncles produced F_1 hybrids with papillate peduncles. The papillae of this hybrid are fewer in number and smaller in size, however, than those of the *T. timopheevi* parent. The peduncles immediately below the spike of *S. fragile* are abundantly pubescent. When this species is crossed with *H. villosa* the resultant hybrids have pubescent peduncles. The hairs of the hybrids, however, are greater in number but slightly shorter than those of the pubescent parent (pl. 2, *A*, *B*, *C*).

5. Glaucous culm is dominant over nonglaucous culm. *Triticum timopheevi*, *T. dicoccoides*, *T. durum*, *T. turgidum*, *T. polonicum*, *Secale fragile*, and *Haynaldia villosa* all have glaucous culms. The culms of *T. aegilopoides* and *T. dicoccum* are not glaucous. When these latter two are crossed with *H. villosa* the F_1 hybrids have glaucous culms.

6. Considerable variation occurs in the length, number, and distribution of hairs on the nodes of the parents and hybrids. In some species considerable variation in hairiness exists even on the separate nodes of the same culm. When *Triticum aegilopoides* and *T. dicoccoides*, with pubescent nodes, are crossed with *Haynaldia villosa*, with glabrous nodes, the F_1 hybrids have nodes with intermediate hair development. *T. timopheevi*, *T. dicoccum*, and *T. polonicum*, with puberulent nodes, when crossed with *H. villosa* produced hybrids with nodal hairs usually shorter and fewer than those possessed by the puberulent parent. *Secale fragile*, with puberulent nodes, when crossed with *H. villosa* produced F_1 hybrids having glabrous nodes. *T. durum* and *T. turgidum* have glabrous nodes.

7. Considerable variation in width of the leaf blades exists among the parents and F_1 hybrids of the various crosses. *Triticum aegilopoides*, with leaves 5 mm in width, represents the narrowest, while *T. polonicum*, with leaves 20 mm in width, represents the widest. *T. timopheevi*, *T. dicoccoides*, *T. durum*, *T. dicoccum*, *T. polonicum*, and *T. turgidum* are all equal to or greater than *Haynaldia villosa* in leaf width. When *T. timopheevi*, *T. dicoccoides*, and *T. durum* are crossed with *Haynaldia*, F_1 hybrids are produced with leaves greater in width than those of either parent. *T. dicoccum*, *T. polonicum*, and *T. turgidum*, when crossed with *Haynaldia*, produced F_1 hybrids with leaves intermediate in width between those of the parents. *T. aegilopoides* and *Secale fragile* are less in leaf width than *Haynaldia*, and hybrids of the former with *Haynaldia* have leaf blades intermediate in width between the parents, while hybrids of the latter with *Haynaldia* have leaf blades less in width than either.

8. Pubescent leaf blade margins are dominant over glabrous leaf blade margins. *Triticum aegilopoides*, *T. timopheevi*, *T. polonicum*, *Secale fragile*, and *Haynaldia villosa* have leaf blades with pubescent margins. *T. dicoccoides*, *T. dicoccum*, *T. turgidum*, and *T. durum* have leaf-blade margins devoid of pubescence. When the four latter are crossed with *Haynaldia* the F_1 hybrids possess pubescence on leaf-blade margins.

9. Scabrid leaf-blade margins are dominant over their absence. *Triticum aegilopoides*, *T. timopheevi*, *T. dicoccoides*, *T. dicoccum*, *T. durum*, *T. polonicum*, *Secale fragile*, and *Haynaldia villosa* have scabrid leaf-blade margins. *T. turgidum* has nonscabrid leaf-blade margins. When the latter is crossed with *Haynaldia*, F_1 plants with scabrid leaf-blade margins result.

10. Pubescent leaf sheaths are dominant over glabrous leaf sheaths. *Triticum dicoccoides*, *T. dicoccum*, *T. durum*, *T. polonicum*, *T. turgidum*, and *Haynaldia villosa* have glabrous leaf sheaths. *T. aegilopoides*, *T. timopheevi*, and *Secale fragile* have pubescent leaf sheaths. When these are crossed with *Haynaldia* the F_1 plants possess pubescence on the leaf sheaths.

11. Glaucous leaf sheaths are dominant over absence of this character. The leaf sheaths of *Triticum aegilopoides* and *T. dicoccoides* are nonglaucous. *T. timopheevi*, *T. dicoccum*, *T. durum*, *T. polonicum*, *T. turgidum*, *Secale fragile*,

and *Haynaldia villosa* have glaucous leaf sheaths. *T. aegilopoides* and *T. dicoccoides*, when crossed with *Haynaldia*, produce hybrids with glaucous leaf sheaths.

12. Anthocyanin pigmentation of the leaf sheaths is dominant over its absence. *Triticum dicoccoides*, *Secale fragile*, and *Haynaldia villosa* have anthocyanin-pigmented leaf sheaths. *T. aegilopoides*, *T. timopheevi*, *T. dicoccum*, *T. durum*, *T. polonicum*, and *T. turgidum* are without anthocyanin pigmentation. When these are crossed with *Haynaldia* the F_1 hybrids have anthocyanin-pigmented leaf sheaths.

13. Pubescence of overlapping leaf-sheath margin is dominant over its absence. *Triticum dicoccum*, *T. durum*, *T. polonicum*, *T. turgidum*, *Secale fragile*, and *Haynaldia villosa* all have overlapping leaf-sheath margins devoid of pubescence. *T. aegilopoides*, *T. timopheevi*, and *T. dicoccoides* have pubescent overlapping leaf-sheath margins. When the three latter are crossed with *Haynaldia* the F_1 hybrids all possess pubescence on the overlapping leaf-sheath margins.

14. The length of the auricle varies among the different species and hybrids. *Triticum aegilopoides* and *T. timopheevi*, with short auricles, crossed with *Haynaldia villosa*, possessing longer auricles, produced F_1 hybrids somewhat intermediate in auricle length between those of the two parents. When *T. dicoccoides*, *T. turgidum*, and *Secale fragile* are crossed with *H. villosa* the F_1 hybrids are similar to the *Haynaldia* parent in auricle length. *T. dicoccum* and *H. villosa* are the same in auricle length, and their F_1 has auricles of the same length as the parents. Crosses of *T. durum* and *T. polonicum* with *Haynaldia* produce F_1 hybrids with auricles greater in length than those of either parent.

15. With the exception of *Triticum polonicum* and *T. durum*, all of the species used in the crosses here reported have hairs on the auricles, these ranging from 0.25 to 6.0 mm in length. *T. aegilopoides*, *T. dicoccum*, and *T. turgidum* crossed with *Haynaldia villosa* produced hybrids having auricle hairs intermediate between those of the two parents. Crosses of *T. timopheevi* and *T. dicoccoides* with *Haynaldia* produced hybrids with auricle hairs greater in length than those of the parents. *T. polonicum*, without auricle hairs, crossed with *Haynaldia* produced an F_1 with auricle hairs greater than those of the *Haynaldia* parent. *T. durum*, without auricle hairs, crossed with *Haynaldia* produced an F_1 having auricle hairs similar to those of *Haynaldia*. *Secale fragile*, with short auricle hairs, crossed with *Haynaldia* produced hybrids with auricle hairs as long as those of the *Haynaldia* parent.

16. The ligules of the various species and hybrids vary in length from 0.7 to 4.0 mm. *Triticum aegilopoides* and *T. timopheevi* crossed with *Haynaldia villosa* produced hybrids with ligules intermediate in length between those of the parents. *T. dicoccoides* and *T. turgidum* crossed with *Haynaldia* produced hybrids having ligules greater in length than those of either parent. *T. durum*, *T. polonicum*, and *Secale fragile* crossed with *Haynaldia* produced hybrids having ligules of the same length as those of the *Haynaldia* parent. The ligules of the F_1 hybrid of the cross *T. dicoccum* × *Haynaldia* are similar in length to those of the *T. dicoccum* parent.

17. The spike widths of the F_1 hybrids are not exactly comparable with those of the parents because of self-sterility. When kernels are present in the florets the glumes are spread apart, causing an increase in the width of the spikelets. The simple type of head of *Triticum turgidum* var. Alaska is 10 mm wide, while the ramified type of the same variety is 35 mm wide. Hybrids of *T. turgidum* × *Haynaldia villosa* produced simple heads with a maximum width of 9 mm or ramified heads with a maximum head width of 35 mm. The F_1 simple head type is about the same width as that of *Haynaldia*, the smaller parent, and the F_1 ramified heads are about the same width as those of the *T. turgidum* parents. In the crosses *T. aegilopoides* × *H. villosa*, *T. dicoccoides* × *H. villosa*, *T. durum* × *H. villosa*, and *Secale fragile* × *H. villosa* the F_1 heads are somewhat intermediate in width between those of the parents. The head width of the F_1 of *T. dicoccum* × *H. villosa* is the same as that of *T. dicoccum*, the smaller parent, and the F_1 head width of the crosses *T. timopheevi* and *T. polonicum* with *H. villosa* is less than that of either parent (pls. 5, 9, 10, 11).

18. Crosses of the various species of *Triticum* and *Secale* with *Haynaldia villosa* produced F_1 hybrids with spikes longer than those of either parent (figs. 1–8).

19. The number of spikelets to a head varies with the parents and hybrids. *Triticum dicoccoides*, with an average of 19 spikelets, represents the species

with the smallest number of spikelets to the head. *T. turgidum*, with an average of 55 spikelets, represents the species with the greatest number of spikelets to the head. When *T. aegilopoides*, *T. timopheevi*, *T. dicoccoides*, *T. polonicum*, and *Secale fragile* were crossed with *Haynaldia villosa* the F_1 hybrids produced a greater average number of spikelets to the head than that produced by either parent. When *T. dicoccum*, *T. durum*, and *T. turgidum* were crossed with *Haynaldia* the F_1 hybrids produced an average number of spikelets intermediate between those of the parents.

20. The spikelets vary in width. The width of the F_1 spikelets resulting from the crosses *Triticum aegilopoides*, *T. dicoccoides*, *T. turgidum*, and *Secale fragile* with *Haynaldia villosa* is greater than that of either parent. The width of the F_1 spikelets resulting from the crosses of *T. timopheevi* and *T. dicoccum* with *Haynaldia* is smaller than that of either parent. The cross of *T. durum* with *Haynaldia* produces a spikelet the width of which is intermediate between the widths of the parents. The width of the F_1 spikelets of the cross *T. polonicum* by *Haynaldia* is equal to that of *T. polonicum*, the larger parent (pls. 5, 9, 10, 11).

21. There is considerable variation in the length of the spikelets of the parents and hybrids. The spikelet measurements were made from the tip of the uppermost floret to the base of the glume of the lowermost floret. Crosses of *Triticum aegilopoides*, *T. dicoccum*, and *T. polonicum* with *Haynaldia* produced F_1 hybrids with spikelets intermediate in length between those of the parents. *T. timopheevi*, *T. dicoccoides*, *T. turgidum*, and *Secale fragile*, when crossed with *Haynaldia*, produced F_1 hybrids greater in spikelet length than that of either parent. The F_1 hybrid of *T. durum* × *H. villosa* produced spikelets equal in length to those of *T. durum*. Characters that materially influence the length of the spikelet are the number and length of the imperfect upper florets. In the species studied, with the exception of *T. aegilopoides*, each of the two lower florets of a spikelet normally produced a kernel. In all the hybrids but one (*T. turgidum* var. Alaska × *H. villosa*) the glumes appeared normal in development but no kernels were produced. The number of imperfect upper florets of a spikelet varies somewhat among the different species. The upper florets of the spikelets of *S. fragile* and *T. aegilopoides* are only rudimentary and do not protrude above the two lower florets. *T. aegilopoides* produces only a single kernel to the spikelet. *Haynaldia* had the greatest number of sterile florets protruding on the spikelet and when crossed with species of *Triticum* and *Secale* usually produced an intermediate expression of this character (pls. 5, 9, 10, 11).

22. Branched rachis is dominant over simple rachis. *Haynaldia villosa* and all the species of *Triticum* studied, with the exception of *T. turgidum*, have simple rachises. *T. turgidum* var. Alaska usually produces ramified or branched heads, but this character is not stable under all environments and both branched and simple head types may be produced. When *T. turgidum* var. Alaska with ramified or branched heads was crossed with *H. villosa* having simple heads, the F_1 hybrids produced both branched and simple heads (fig. 7).

23. Fragile rachis is dominant over tough rachis. Fragility of the rachis has been divided into two types of expression, i. e., fragile and very fragile. *Triticum aegilopoides*, *T. dicoccoides*, *Secale fragile*, and *Haynaldia villosa* have very fragile rachises. *T. dicoccum* has a fragile rachis. *T. timopheevi*, *T. durum*, *T. polonicum*, and *T. turgidum* have tough rachises. Species with fragile rachises crossed with *H. villosa*, having a very fragile rachis, produced F_1 hybrids with very fragile rachises. Species with tough rachises crossed with *H. villosa* produced F_1 hybrids with very fragile rachises. The one exception to this was the F_1 hybrid of the cross *T. polonicum* × *H. villosa*, which produced fragile rachises (pls. 5, 9, 10, 11).

24. All the species of *Triticum* and *Secale* used in crosses, with the exception of *T. timopheevi*, have oblong or wedge-shaped rachis internodes. When these were crossed with *H. villosa*, with obovate rachis internodes, the F_1 hybrids had intermediate-shaped internodes. *T. timopheevi*, with blunt cuneate-shaped rachis internodes, when crossed with *Haynaldia*, produced F_1 hybrids with rachis internodes intermediate between those of the parents. In plate 8, *A*, is shown an oblong rachis internode of *T. dicoccoides;* plates 8, *C*, shows an obovate rachis internode of *H. villosa;* plate 8, *B*, the F_1 hybrid between the two forms. As may be observed, the F_1 hybrid favors the *Triticum* parent in length, while the obovate condition of the *Haynaldia* rachis predominates.

25. The rachis internodes of the various parents and F_1 hybrids vary in length. When *Triticum aegilopoides* and *T. durum* with long rachis internodes

were crossed with *Haynaldia villosa* with short rachis internodes, the internodes of the F_1 hybrids were the same length as the internodes of the *Triticum* parents. *T. timopheevi*, with the short rachis internodes, when crossed with *Haynaldia*, produced F_1 hybrids with internodes longer than those of either parent. *Secale fragile*, *T. dicoccoides*, and *T. polonicum*, with long internodes, when crossed with *Haynaldia* produced F hybrids with internodes intermediate between those of the parents. The F_1 hybrids of the crosses *T. turgidum* and *T. dicoccum* with *Haynaldia* produced rachis internodes greater in length than those of the *Triticum* parent.

26. The nontufted condition of hairs on the lateral edges of the rachis internodes is dominant over the tufted condition. All of the species of *Triticum* and *Secale* studied have nontufted hairs on the lateral edges of the rachis internodes, and, while *Haynaldia* has rachis internodes with tufted hairs, the F_1 hybrids all had nontufted hairs (pls. 5, 9, 10, 11).

27. Glume width varies among the different species and hybrids. The glumes of the F_1 hybrids of *Triticum timopheevi*, *T. aegilopoides*, and *Secale fragile* with *H. villosa* are intermediate in width between the glumes of the parents. F_1 hybrids of *T. durum* and *Haynaldia* have glumes equal in width to those of *Haynaldia*, the parent with widest glumes. The F_1 hybrids of *T. polonicum* and *Haynaldia* are equal to *T. polonicum* in width of glume. The glume width of the F_1 hybrids of *T. turgidum* and *T. dicoccum* with *Haynaldia* is greater than that of either parent. The glumes of *T. dicoccoides*, *H. villosa*, and their hybrids are alike in width.

28. Glume length varies among the species and hybrids. Crosses of *Triticum timopheevi*, *T. dicoccoides*, *T. polonicum*, and *Secale fragile* with *Haynaldia* produced hybrids the glume length of which was intermediate between that of the parents. When *T. aegilopoides*, *T. dicoccum*, *T. durum*, and *T. turgidum* are crossed with *Haynaldia*, the F_1 glume length is greater than that of either parent.

29. The beaks or awns on the glumes of the several species of *Triticum* and of *Secale* and *Haynaldia* and their hybrids vary considerably in length. All of the *Triticum* species studied have shorter glume beaks than those of *Haynaldia*. The glume beaks of the F_1 hybrids of *T. timopheevi*, *T. dicoccoides*, and *T. dicoccum* are greater in length than those of the parents. F_1 hybrids of *T. aegilopoides*, *T. durum*, and *T. turgidum* have glume beaks intermediate between those of the parents but favor *Haynaldia*. The F_1 hybrid of *T. polonicum* and *Haynaldia* has glume beaks as long as those of *Haynaldia*, the parent with the longer glume beaks. The glume beaks of the F_1 hybrid of *S. fragile* and *Haynaldia* are intermediate between those of the parents but favor those of *Secale*.

30. Considerable variation occurs in the shape of the glumes at the apex and in the expression of the tooth when present. *Haynaldia villosa* has broad, elevated, and rounded shoulders. *Secale fragile* lacks glume shoulders, and when crossed with *H. villosa* it produced F_1 hybrids with glume shoulders slightly elevated and somewhat intermediate in width. When *Triticum durum*, with narrow and slightly elevated glume shoulders, was crossed with *H. villosa*, the F_1 hybrids had shoulders that were elevated and intermediate in width *T. turgidum*, with narrow and oblique glume shoulders, crossed with *H. villosa*, produced F_1 hybrids having elevated glume shoulders intermediate in width. *T. monococcum* and *T. dicoccum*, with narrow glume shoulders and a short tooth, crossed with *Haynaldia*, produced F_1 hybrids having glume shoulders intermediate in width and possessing a tooth on each glume. *T. dicoccoides* and *T. timopheevi*, with glume shoulders slightly elevated and with a single tooth, when crossed with *Haynaldia*, produced F_1 hybrids with usually slightly elevated glume shoulders intermediate in width and sometimes showing a rudimentary tooth (pls. 5, 9, 10, 11).

31. *Haynaldia villosa* has large papillae on its glumes. When crossed with *Triticum aegilopoides*, *T. dicoccoides*, *T. durum*, *T. dicoccum*, *T. turgidum*, *T. polonicum*, and *Secale fragile*, all with small papillae, it produced F_1 hybrids with intermediate-sized papillae on their glumes. *T. timopheevi*, with glumes devoid of papillae, when crossed with *Haynaldia* produced F_1 hybrids with medium-sized papillae on their glumes.

32. Canaliculate glumes are dominant over the noncanaliculate condition. *Haynaldia villosa* possesses a deep channel or depression between the two prominent keels of the glume. No channels of this nature are present in the other species studied. The crosses all showed the canaliculated condition in the F_1 hybrids, except that the glumes had more shallow depressions than *H.*

villosa and were usually bisected by a prominent nerve, forming two distinct channels. *Secale frigile* × *H. villosa* had no middle nerve. Unicanaliculation is always associated with bicarination.

33. Bicarinate glumes are dominant over unicarinate glumes. All of the *species of Triticum* and *Secale* reported herein are single-keeled or unicarinate, while *Haynaldia villosa* has bicarinate glumes. There is some variation in the keel expression of the bicarinate glumes of the F_1 hybrids, but, in general, the bicarinate condition predominates.

34. Glaucous glumes are dominant over nonglaucous glumes. *Haynaldia villosa*, *Triticum timopheevi*, *T. polonicum*, *T. turgidum*, *T. durum*, and *Secale fragile* have glaucous glumes, and hybrids involving them all had glaucous glumes. *T. dicoccum*, *T. acgilopoides*, and *T. dicoccoides* have nonglaucous glumes, yet when crossed with *H. villosa* the hybrids had glaucous glumes. The hybrids usually were glaucous, intermediate in degree between the parents.

35. Pubescent glumes and lemmas are dominant over nonpubescent glumes and lemmas. All of the species studied, except *Triticum polonicum* and *T. timopheevi*, have nonpubescent glumes and lemmas. The two exceptions have pubescence on the exterior surface of the glumes. The presence of pubescence on the glumes and lemmas of these forms is accompanied by the additional development of asperites and hairs (pubescence) of greater thickness and length on the keels and nerves. This is true to an extent that hairs sometimes resemble small superasperites (pl. 9). When *Haynaldia*, with glabrous glumes and tufted bristles on its keels, is crossed with *Triticum timopheevi*, with pubescent glumes and asperites on its keels, the F_1 hybrids have glumes with considerably reduced pubescence both in length of hair and distribution, and keels with superasperites 1.7 mm long. On the other hand, when *Haynaldia* is crossed with *T. polonicum*, with less pubescence than that possessed by *T. timopheevi*, the F_1 hybrids have a reduced pubescence on the glumes with only slight development of asperites on the keels and prominent nerves. These asperites rarely exceed 0.5 mm in length. A few superasperites as long as 1.5 mm, however, were sometimes developed on the keel of the lemma.

36. The lemmas of the different species and F_1 hybrids are variable in width. When *Haynaldia villosa* was crossed with *Triticum aegilopoides*, the F_1 hybrids had lemmas equal in width to those of *Haynaldia*, which had the widest lemmas. The F_1 hybrids of *T. dicoccoides* have lemmas equal in width to those of the parents. The F_1 lemma widths of the crosses *T. durum* and *T. turgidum* with *Haynaldia* are greater than those of either of the parents. The F_1 hybrids of the cross *Secale fragile* with *Haynaldia* have lemmas equal in width to those of *S. fragile*, the parent having the wider lemmas. The F_1 hybrids of the cross *T. dicoccum* × *H. villosa* have lemmas as wide as those of *T. dicoccum*, the wider parent.

37. The lemmas of all the species and hybrids vary in length. In all the crosses but one the F_1 hybrids produced lemmas intermediate in width between those of the parents. The exception, the cross *Triticum dicoccum* × *H. villosa*, produced F_1 hybrids with lemmas slightly greater in length than those of either parent.

38. The awns on the lemmas of the various species and their hybrids show considerable variation in length. Crosses of *Triticum aegilopoides*, *T. timopheevi*, *T. dicoccoides*, *T. durum*, *T. polonicum*, *T. turgidum*, *T. dicoccum*, and *Secale fragile* with *Haynaldia villosa* produced F_1 hybrids with lemma awns intermediate in length between those of the parents.

39. Black or purple awns on lemmas and glumes are dominant over yellow awns. When black-awned species are crossed with purple-awned species, the awns of the hybrids are usually purplish black. *Triticum timopheevi*, *T. dicoccoides*, *T. polonicum*, and *T. turgidum* have brown to black awns, while *T. aegilopoides*, *T. dicoccum*, and *T. durum* have yellow awns. When *Haynaldia villosa* with purple pigment in its awns was crossed with *T. aegilopoides*, *T. dicoccum*, or *T. durum*, the F_1 hybrids produced weakly purple awns. When *H. villosa* was crossed on *T. timopheevi*, *T. dicoccoides*, *T. polonicum*, or *T. turgidum*, the F_1 hybrids had purplish black awns. *Haynaldia* crossed with *Secale fragile*, also having purple awns, produced F_1 hybrids with awns usually more intensely purple than those of either parent.

40. *Haynaldia villosa* has large papillae on its lemmas. When crossed with *Triticum aegilopoides*, *T. timopheevi*, *T. dicoccoides*, *T. durum*, *T. dicoccum*, *T. turgidum*, *T. polonicum*, and *Secale, fragile*, all with small papillae, F_1 hybrids were produced with intermediate-sized papillae on their lemmas. In plates 2, *D*, and 11 *F*. are shown papillae on a lemma of H. villosa.

41. In general, the trichomes on the glume keels of the F_1 hybrids resulting from crosses between species having short and long glume keel trichomes are intermediate in length. When *Triticum* species possessing glumes with asperites on their keels were crossed with *Haynaldia*, which possesses bristles on its glume keels, the F_1 hybrids had superasperites on the keels (pls. 5, 9, 10, 11, 12). *Secale fragile*, with asperites on its glume keels, when crossed with *Haynaldia*, produced F_1 hybrids with superasperites on their glume keels slightly shorter than those on the *Triticum* hybrids (pls. 10, 14).

42. Nontufted or continuous trichomes on the glume keels are dominant over tufted trichomes. Nontufted trichomes are present on the glume keels of the species of *Triticum* and *Secale* studied. When they were crossed with *Haynaldia*, which has tufted trichomes on its glume keels, the F_1 hybrids had nontufted trichomes or superasperites on their glume keels. These superasperites were usually fewer, thicker, and shorter than the tuft bristles on the glume keels of *Haynaldia* (pls. 5, 9, 10, 11, 12, 14).

43. *Triticum aegilopoides*, *T. timopheevi*, *T. dicoccoides*, *T. dicoccum*, *T. durum*, *T. polonicum*, and *T. turgidum* have short trichomes or asperites on the keels of their lemmas. When crossed with *Haynaldia villosa*, having long trichomes or bristles on the keels of its lemmas, these species produced F_1 hybrids with superasperites intermediate in length between the trichomes of the parents (pls. 5, 9, 10, 11, 12). *Secale fragile*, with spur asperites on its lemma keels, when crossed with *H. villosa* produced F_1 hybrids with superasperites intermediate between the trichomes of the parents (pls. 9, 14).

44. Nontufted or continuous trichomes on the lemma keels are dominant over tufted trichomes. Nontufted trichomes are present on the lemma keels of the species of *Triticum* and *Secale* studied. When these species were crossed with *Haynaldia*, which has tufted trichomes on its lemma keels, the F_1 hybrids had nontufted trichomes or superasperites on their lemma keels. These superasperites were usually fewer, thicker, and shorter than the tuft bristles on the lemma keels of *Haynaldia* (pls. 5, 9, 10, 11, 12, 14).

45. At the base and on the exterior side of the spikelets of the various species and hybrids are short bristles varying in length from 0.2 to 5 mm. *Triticum aegilopoides*, *T. timopheevi*, *T. dicoccoides*, *T. dicoccum*, *T. durum*, *T. polonicum*, and *T. turgidum* have basal bristles considerably longer than those of *Haynaldia villosa*. When these species were crossed with the latter, the F_1 hybrids had basal bristles intermediate in length between those of the parents. *Secale fragile*, with basal bristles 0.2 mm long, produced F_1 hybrids with basal bristles 0.35 mm long. Plate 6 shows the basal bristles of the parents and F_1 hybrid of the cross *T. dicoccoides* × *H. villosa*.

46. In general, the number of bristles at the base and on the exterior side of the rachis of the F_1 hybrids is intermediate between those of the parents, but tends toward the condition in the *Triticum* or *Secale* parent (pls. 6, 7).

47. At the base of the spikelet on the side facing the rachis the various species and F_1 hybrids possess short bristles varying in length from 0.2 to 1.5 mm. *Triticum aegilopoides*, *T. dicoccum*, and *T. turgidum*, with bristles 0.3 mm long, produced F_1 hybrids with bristles equal in length to those of the *Triticum* parent. *T. durum*, *T. polonicum*, and *Secale fragile*, with basal bristles equal to or longer than those of *Haynaldia*, when crossed with the latter gave F_1 hybrids with bristles longer than those of either parent. *T. timopheevi* and *T. dicoccoides*, with basal bristles much longer than those of *Haynaldia*, when crossed with the latter gave F_1 hybrids with basal bristles intermediate in length between those of the parents. Plate 7 shows the basal bristles of the parents and F_1 hybrid of the cross *T. dicoccoides* × *H. villosa*.

48. In general, the number of bristles at the base on the side of the spikelets facing the rachis of the F_1 hybrids is intermediate between those of the parents but tends toward the condition in the *Triticum* or *Secale* parent (pls. 6, 7).

49. The F_1 hybrids of the crosses *Triticum aegilopoides*, *T. timopheevi*, and *Secale fragile* with *Haynaldia villosa* had lodicules intermediate in width between those of the parents. F_1 hybrids of the crosses *T. dicoccum* and *T. durum* with *H. villosa* had lodicules greater in width than those of the parents. The cross *T. polonicum* × *H. villosa* produced F_1 hybrids with lodicules as wide as those of the *T. polonicum* parent. In the cross *T. turgidum* × *H. villosa* the F_1 lodicule width was as great as that of the *Haynaldia* parent. The F_1 hybrids of the cross *T. dicoccoides* × *H. villosa* had lodicules similar in width to those of the parent (pl. 13).

50. The length of the lodicules of the various species of *Triticum*, *Secale fragile*, *Haynaldia villosa*, and their hybrids varies. Hybrids of the crosses

T. aegilopoides, *T. timopheevi*, *T. dicoccoides*, *T. durum*, and *T. turgidum* with *Haynaldia villosa* produced lodicules intermediate in length between those of the parents. F_1 hybrids of *T. polonicum* × *H. villosa* produced lodicules longer than those of the parents. F_1 hybrids of *T. dicoccum* × *H. villosa* had lodicules as long as those of *Haynaldia*, the longer parent. The F_1 hybrids of *S. fragile* × *H. villosa* had lodicules as long as those of the *Secale* or longer parent (pl. 13).

51. The length of the hairs on the lodicules is variable. Short hairs are present on both the exterior surface and edges of the lodicules of the *Triticum* species. *Secale fragile* has long hairs confined mostly to the edges of the lodicules, and *Haynaldia villosa* has lodicules with only a few very short hairs on the edges or none at all. The species of *Triticum* and *Secale* used in the crosses had hairs with a maximum length of 1.35 mm on their lodicules, while *H. villosa* had lodicule hairs with a maximum length of 0.05 mm. With the exception of the F_1 hybrids from the crosses *T. aegilopoides* and *T. dicoccoides* with *H. villosa*, all the crosses produced F_1 hybrids with lodicule hairs intermediate in length between those of the parents. The two exceptions produced F_1 hybrids with lodicule hairs longer than those of the *Triticum* or longer parent (pl. 13).

52. *Triticum aegilopoides* has paleas that are split laterally through the center. All of the other species of *Triticum*, *Secale fragile*, and *Haynaldia villosa* have entire paleas. When *T. aegilopoides*, with split paleas, was crossed with *H. villosa*, the F_1 hybrids produced entire paleas.

The only F_1 hybrid involved in the experiments herein reported that produced seed was that from the cross *Triticum turgidum* var. Alaska × *Haynaldia villosa*. The kernels of this F_1 hybrid are longer than those of either parent and somewhat intermediate in width. The kernels of the F_2 plants are similar in size to those of the F_1 plants. Plate 2 shows characteristic kernels of the parents and of the F_1 and F_2.

With the exception of the cross *Triticum turgidum* var. Alaska × *Haynaldia villosa*, no material is available for study beyond the F_1 generation, owing to self-sterility. However, the variability in the expression of the characters of the parents and their behavior in the F_1 hybrids suggests different modes of inheritance. The following characters show a quantitative expression: Plant stature, leaf width, auricle length, auricle hair length, ligule length, width and length of spike, number of spikelets, width and length of spikelets, length of rachis internodes, length and width of glumes, length of glume beak, length and width of lemma, awn length, length of trichomes on glume and lemma keels, length of bristles at base of spikelet on exterior side and on side facing rachis, width and length of lodicule, and length of lodicule hairs.

The characters that are extremely difficult or impossible to measure at the present time, but which, by inspection, also showed differences in expression of quantitative nature are as follows: Solidity of straw, anthocyanin in culm and leaf sheath, glaucousness of culm and leaf sheaths, pubescence of culm nodes and glumes, scabrousness of leaf-blade margins, pubescence of leaves and leaf sheaths, glaucousness of glumes, fragility of rachis, shape of shoulder on glume, canaliculation of glumes, carination of glumes, black and purple pigmentation of the awns, and number of bristles at the base of the spikelet on exterior and interior sides.

Other characters that suggest simple inheritance based on single-factor differences are pubescence of the peduncle, pubescence on the overlapping edge of leaf sheaths, branching of rachis, size of papillae on lemma and glume, arrangement of trichomes (tufting) on glume and lemma keels, and split palea.

SUMMARY

Haynaldia villosa was crossed on *Triticum aegilopoides*, *T. timopheevi*, *T. dicoccoides*, *T. dicoccum*, *T. durum*, *T. polonicum*, *T. turgidum*, and *Secale fragile*, and the F_1 plants were matured. Attempts also were made to cross *H. villosa* with *T. vulgare*, *T. compactum*, *T. spelta*, *S. cereale*, and *S. cereale ancestrale*, but only an occasional enlarged structure, with neither embryo nor endosperm, was produced. However, one hybrid seed of the cross *T. vulgare* (C. I. 6223) × *H. villosa* germinated but the plant died before the formation of the third leaf.

All the F_1 plants except those of the cross *Triticum turgidum* var. Alaska × *Haynaldia villosa* were completely self-sterile. The F_1 hybrids of this cross produced an average seed set of 3.8 percent, with a maximum of 11.1 percent for a single plant. The F_2 plants produced an average seed set of 29.7 percent, with a maximum of 58.8 percent for a single plant. The F_3 plants produced an average seed set of 58.5 percent, with a maximum of 76.9 percent for a single plant. No apparent segregation occurred in the F_2 and subsequent generations, the F_1 type remaining fixed in its morphological characters.

In general, most of the F_1 hybrids resulting from the crossing of *Triticum* species and *Secale fragile* with *Haynaldia villosa* resembled the *Triticum* or *Secale* parent, but a critical study of the morphological characters possessed by the parents and the F_1 hybrids indicates that the majority of the characters of the hybrids are intermediate between those of the parents. Some characters of the F_1 plants show, however, a decided increase in degree of expression over those of either parent, while others show a dominance of the one or the other parent.

More than 52 morphological characters of the parents and the F_1 hybrids of eight crosses were studied in detail.

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A CYTOLOGICAL STUDY OF PUCCINIA MALVACEARUM FROM THE SPORIDIUM TO THE TELIOSPORE[1]

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INTRODUCTION

As knowledge of heterothallism in the rusts broadens and the importance of the spermogonium in reproduction is realized, the question arises as to how reproduction takes place in rusts that have no spermogonia.

Hollyhock rust, *Puccinia malvacearum* Bert., a microcyclic species without spermogonia, was chosen for study. The rust is maintained by a succession of telial generations. Aecia, uredia, and spermogonia are unknown. An earlier paper (*5*)[3] on this rust presents cytological details of the development of the teliospore, nuclear fusions within it, the germination of the spore, the reduction divisions, and the formation of the sporidia. The present study begins with the sporidium and traces the infection of the host, mycelial growth, and the development of the telial sorus.

The literature on *Puccinia malvacearum* was reviewed in the former paper (*5*). A few additional notes are given here.

Before the discovery of heterothallism in rusts (*18*), in 1927, homothallism was taken for granted. On the assumption that the binucleate mycelium could arise directly within an isolated haploid mycelium, the main cytological interest in both long- and short-cycle rusts centered on the mode of transition to the binucleate condition. Several papers deal with this point in *Puccinia malvacearum*.

Blackman and Fraser (*15*), in 1906, found that the transition from uninucleate to binucleate cells in *Puccinia malvacearum* took place at several points in the same sorus and suggested the possibility that two sister nuclei may become conjugate in a cell. They also state (*15, p. 42*) that —

> The smallness of the cells and nuclei, and the absence of any regular row or group of cells—such as are found in the aecidia—on which attention can be concentrated in the hunt for nuclear migrations or cell-fusions, render the task of elucidating such a point almost hopeless.

Olive (*29*), in 1911, noted that in some short-cycle rusts the binucleate mycelium arises at the base of the sorus and that in others it "arises at some indefinite point earlier in the life history in the vegetative mycelium." *Puccinia malvacearum* is listed in the first group.

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[3] Reference is made by number (italic) to Literature Cited, p. 816.

Werth and Ludwigs (*32*), in 1912, found that in the young sorus of *Puccinia malvacearum* there is a definite layer of column-shape cells. These form pairs, each consisting of a smaller and a larger cell, and the nucleus of the smaller cell passes through a small opening in the walls into the larger cell. They also note an occasional irregular binucleate cell in the tissue above.

Moreau (*28*), in 1914, also found a layer of club-shape cells in the young sorus. These fuse by pairs, the wall between the two dissolving first at the tip, then through a broader contact area. The two cells that fuse may be either equal or unequal. The fusion cell gives rise to a short hypha of binucleate cells, at the tip of which the teliospore forms.

Lindfors (*26*), in 1924, also working on *Puccinia malvacearum*, saw fusions at an earlier stage, before the pseudoparenchyma of the sorus formed, and found that the cells that fuse may be equal or unequal. These earlier binucleate cells grow and divide further before spore formation.

As may be seen, these accounts of the origin of the binucleate cells in *Puccinia malvacearum* contradict each other on nearly every point.

Since the discovery of heterothallism in rusts, it still has been assumed that a microcyclic species without spermogonia would be without means of crossing and so must be homothallic. Jackson (*24*), in 1931, and Buller (*17, p. 286*), in 1931, cite *Puccinia malvacearum* as probably homothallic, and Ashworth (*12*), in 1931, presents experiments in support of homothallism.

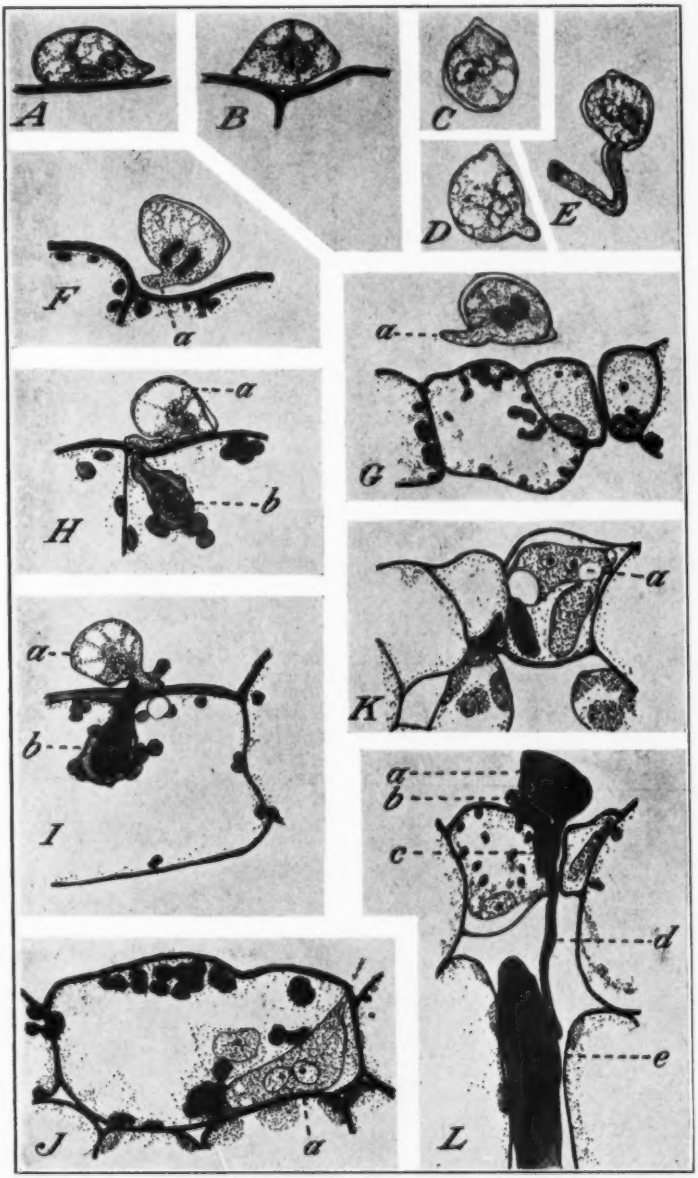
MATERIAL AND METHODS

Potted mallow (*Malva* sp.) plants were used for inoculation. Some were grown and inoculated in the greenhouse; others out of doors on a third-floor balcony. In inoculation, a glass cylinder 4 inches in diameter and 8 or 10 inches high, lined with wet paper toweling, was set down over the plant with the lower edge pressed into the soil. A pad of wet paper was placed in a Petri dish and an infected leaf of hollyhock (*Althaea rosea* (L.) Cav.) or mallow was placed on it and secured in position by rubber bands. This was inverted and placed on the top of the cylinder as a lid. A layer of wet paper was folded down about the top, covered with cellophane, and fastened in place by a rubber band. This placed the germinating spores directly over the mallow plant in a small damp chamber. The plant was then heavily watered and placed in diffuse light for 48 hours; then the cylinder was removed and the plant was placed in stronger light. Attempts were made to keep the plants free of insects.

Material was fixed daily up to 12 days after inoculation and at longer intervals from then until 25 days after inoculation. Several fixing solutions were tried, but Flemming's medium and weak solu-

EXPLANATORY LEGEND FOR PLATE 1

A, B, C.—Mature binucleate sporidia 1 day after inoculation was set up. × 1,400.
D, E.—Germinating sporidia, 1 day after inoculation was set up. × 1,400.
F, G.—Sporidia on leaf, each with germ tube, *a*, 1 day after inoculation was set up. × 1,400.
H.—Cytoplasm from sporidium, *a*, flowing into host cell at *b*; 1-day infection. × 1,400.
I.—Germinating sporidium at *a*. Beginning of primary hypha at *b*. One-day infection. × 1,400.
J.—Unicellular, binucleate primary hypha, *a*, from 1-day infection. × 1,400.
K.—Young primary hypha, *a*, in guard cell of stoma; 1-day infection. × 1,400.
L.—Sporidium, *b*, has entered guard cell at *c*. Sporidium, *a*, has entered stomatal aperture. Sporidium, *a*, germ tube, *d*, and palisade cell, *e*, are dead. Three-day infection. × 1,400.



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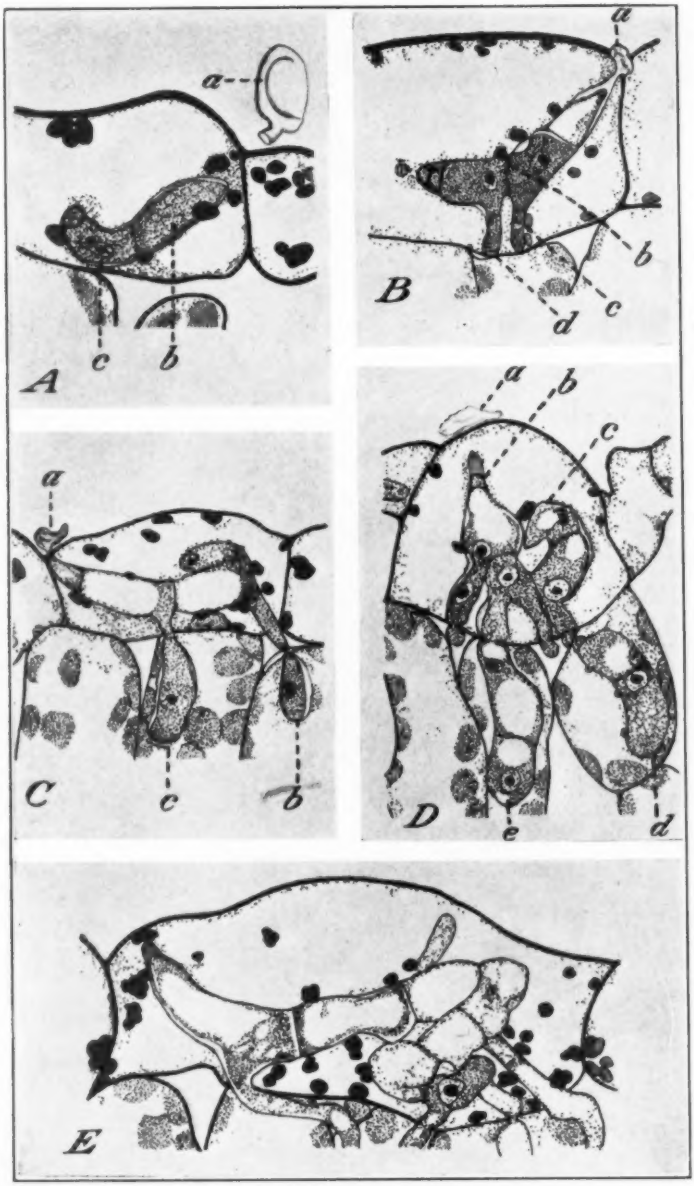

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tions proved the best. The fixed material was washed, dehydrated, and embedded in paraffin. The principal stain used was iron haematoxylin counterstained with Congo red.

In the search for conidia, both potted material and separate leaves of mallow and hollyhock were placed in damp chambers. Material was removed at different times during the day and night; part of it was fixed, and the rest was used in making freehand sections.

EXPERIMENTAL RESULTS

ENTRANCE AND VEGETATIVE GROWTH

During the first 24 hours after an inoculation is set up, the teliospores germinate and produce the sporidia, which fall upon the leaves of the host plant, germinate there, and enter the epidermal cells of the leaf.

The single nucleus of the immature sporidium of *Puccinia malvacearum* divides once (*5*) as the spore matures. Sporidia that have been discharged from the promycelium and are found lying on the host leaf are regularly binucleate (pl. 1, *A*, *B*, *C*).[4] The spore is originally lemon-shape (*C*) but quickly flattens down against the epidermis (*A*, *B*) and pushes out a germ tube at one side (*D*; *F*, *a*; *G*, *a*). This germ tube usually is short, but occasionally (*E*; *L*, *d*) exceeds the diameter of the spore in length.

The tip of the germ tube penetrates the outer wall of the epidermal cell directly (pl. 1, *H*) and enters the host cell. In *H* the cytoplasm is flowing through the germ tube into the host cell (*H*, *b*), leaving the sporidium (*a*) somewhat vacuolated. In *I*, there are 2 spores, 1 of which (*a*) has germinated but not entered, while the other (with spore wall missing) has formed a sack-shape mass (*b*) inside the epidermal cell. Then the two sporidial nuclei move in (*J*, *a*), completing the transfer of the sporidial protoplast to the epidermal cell. The empty, collapsed sporidial wall (pl. 2, *A*, *a*; *B*, *a*; *C*, *a*; *D*, *a*) is often found at the point of entrance.

Ordinarily, the sporidium germ tube enters the epidermal cell on which the sporidium lies. This small thin-walled, short-lived cell with watery content and the minimum of food is incapable of producing a germ tube long enough to grow to a stoma. Even when, by chance, the sporidium falls upon a stoma, it may enter the guard cell instead of growing in through the stomatal aperture. In plate 1, *K*, which shows a diagonal section through a stoma, a portion of a badly cramped primary hypha is seen in the little guard cell at *a*. Perhaps when the sporidium landed the stoma was closed. Rarely, the germinating sporidium does enter the stomatal aperture. *L* shows two

[4] With the exception of plate 5, *A* and *B*, drawings are oriented in the plates as the tissues drawn were oriented in the leaf, i. e., the part drawn that was nearest the upper epidermis of the leaf becomes the upper edge of the drawing.

EXPLANATORY LEGEND FOR PLATE 2

A.—At *a*, empty sporidial wall; *b*, enucleate and, *c*, binucleate cells of primary hypha of 1-day infection. × 1,400.

B.—Primary hypha with empty sporidial wall at *a*, and septum at *b* dividing former binucleate cell into two uninucleate cells which have produced the branches, *c*, *d*; 2-day infection. × 1,400.

C.—Four-cell primary hypha with sporidial wall at *a*, and branches in palisade cells at *b* and *c*; 2-day infection. × 1,400.

D.—Primary hypha, *b*, *c*, with sporidial wall at *a*, and branches in palisade cells at *d* and *e*; 3-day infection. × 1,400.

E.—Older primary hypha from 5-day infection. × 1,400.

sporidia that fell upon the same stoma; the germ tube of one (*b*) entered the guard cell at *c*, while that of the other (*a*) grew in through the stomatal aperture. The venture was not a success. The stoma closed, pinching the germ tube. The sporidium (*a*), the germ tube (*d*), and even the palisade cell (*e*), which was in contact with the germ tube, have died.

The fungus newly entered in an epidermal cell (pl. 1, *J*, *a*) is unicellular and binucleate. It grows rapidly into a multicellular primary hypha. The first septum (pl. 2, *A*) divides the fungus into two nearly equal cells, the one nearest the point of entry (*b*) being without a nucleus, the other (*c*) being binucleate.

During the second day after inoculation, the primary hypha grows apically, becoming curled up in the epidermal cell. A second septum (pl. 2, *B*, *b*) soon cuts the binucleate cell into uninucleate cells, the terminal one of which continues the growth and divides again. *C* shows a 4-cell primary hypha. Early in this development the primary hypha branches. In *B* branches from the second and third cells (*c*, *d*) have grown down to the inner epidermal wall, and in *C*, *b*, *c*, the two branches have grown on into palisade cells, each taking with it the nucleus of the cell from which it grew. In *D* (from 3-day material) the primary hypha (*b*, *c*) has given rise to at least 4 branches, 2 of which have formed large, 2-cell hyphae (*d*, *e*) in palisade cells. Here the nuclear behavior seems to have been different from that shown in *C*, for each cell of the primary hypha still possesses a nucleus, except, of course, the first cell (*D*, *b*), which is now much shrunken.

When the epidermal cell containing a primary hypha is large, the primary hypha may continue to grow. In plate 2, *E* (from a 5-day infection), the richly branched primary hypha is made up of 7 or 8 cells. Sooner or later, however, the primary hypha deteriorates. It can rarely be identified with certainty after the ninth day.

Contrary to what is usually seen in rusts, the mycelium of *Puccinia malvacearum* is not strictly intercellular. Hyphae grow into and through the host cells with comparative freedom. In plate 3, *A*, a branch from a primary hypha entered a palisade cell at *a*, formed there a branching hypha of eight cells, from which at *b* and *d* branches passed into other palisade cells, while at *c* a branch grew out into a large intercellular space and branched rapidly there. Intracellular mycelium is coarser than intercellular mycelium; its cells have about twice the diameter of the intercellular growth. Intracellular growth permeating several palisade cells is shown in *B*. One branch from a primary hypha at *a* formed a slender intercellular hypha (*a*, *d*), from which at *c* a branch grew through one palisade cell into a second at *b*. A dozen or more palisade cells may be invaded in this fashion by branches from a single primary hypha. In plate 3, *C*, *D*, and plate 4, *A*, are shown further examples of the coarse, branching, intracellular hyphae in palisade cells.

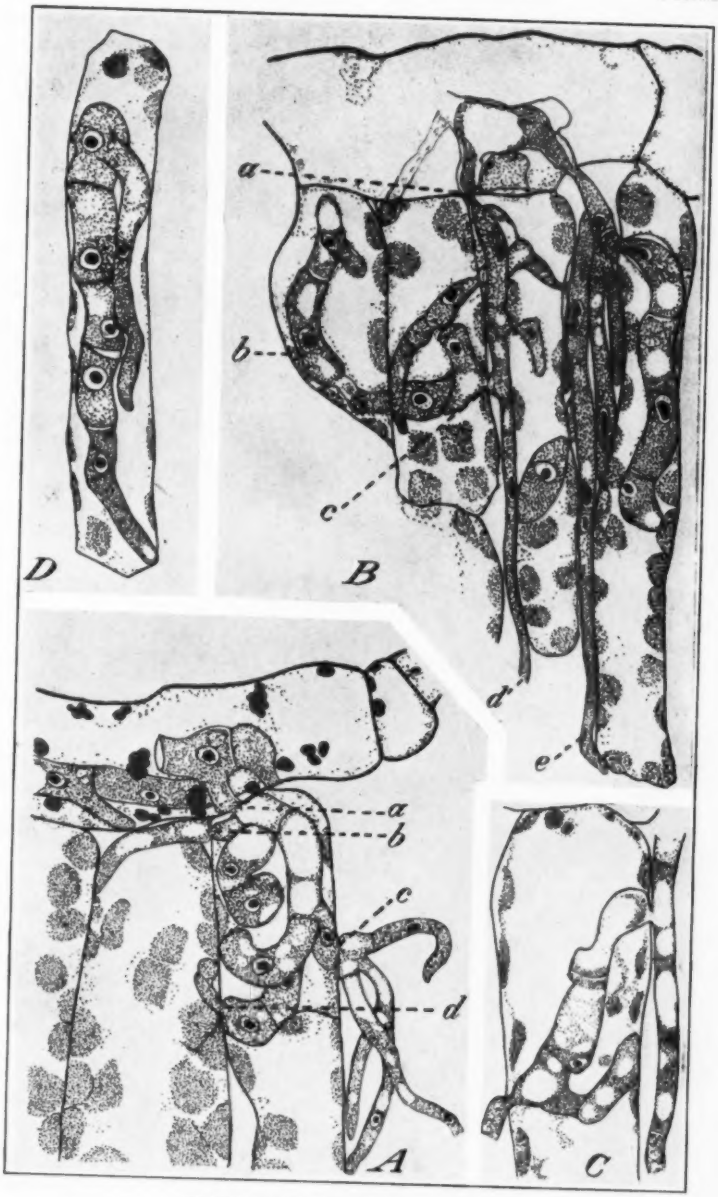
This intracellular habit is not limited to the early mycelial development. In plate 4, *B*, is shown a much-curved branching hypha of

EXPLANATORY LEGEND FOR PLATE 3

A.—A branch from a primary hypha at *a* gave rise to an intracellular hypha in a palisade cell with branches to other palisade cells at *b* and *d*, and a branch to intercellular spaces at *c*; from 5-day infection. × 1,400.

B.—Intercellular mycelium at *a*, *d*, and at *e*, and intracellular hypha, *b*, *c*; 3-day infection. × 1,400.

C, *D*.—Intracellular hyphae in palisade cells from 6-day infection. × 1,400.



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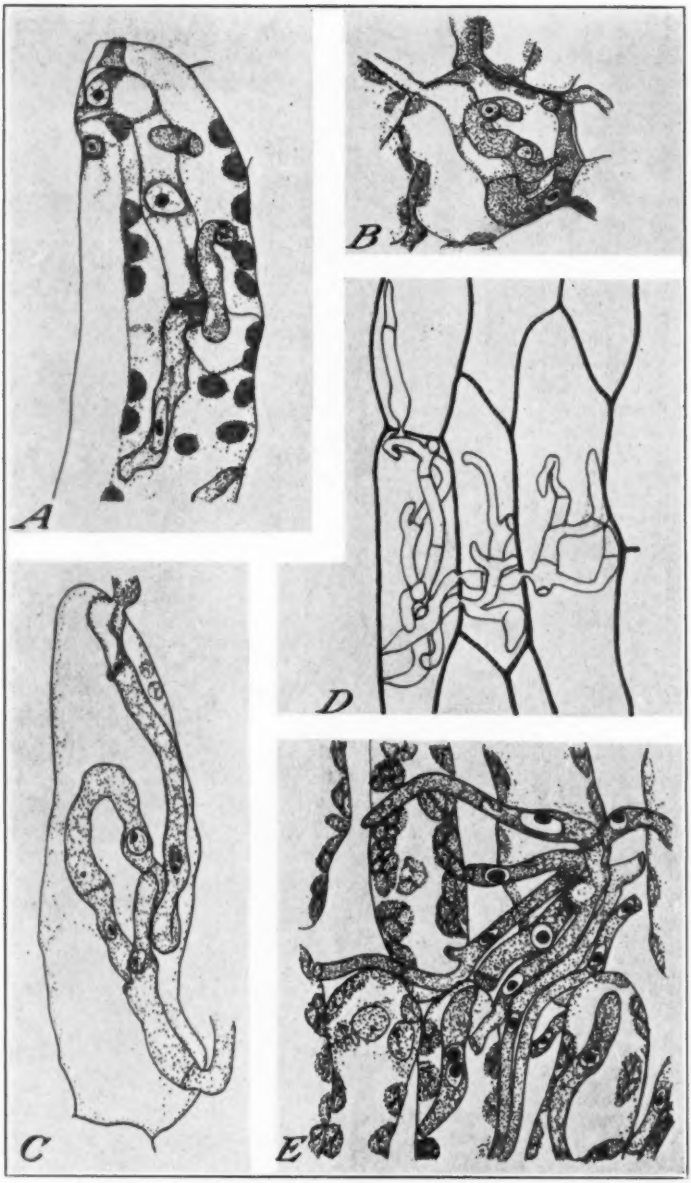

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5 or 6 cells in a spongy mesophyll cell, and in *C* a branching hypha in a large bundle-sheath cell. Similar hyphae often are found in the cells of the lower epidermis. These intracellular hyphae doubtless serve as haustoria in extracting food for the fungus, but they are more than haustoria, for they frequently grow through a host cell and out into intercellular spaces again. Their effect upon the host cell, too, is more severe than that of ordinary haustoria; invaded cells may die sooner.

Some intercellular growth is found between palisade cells near the point of entrance (pl. 3, *A, c; B, d, e*). From here the hyphae spread downward. Plate 4, *E*, shows a richly branching group of intercellular hyphae radiating out into the mesophyll area and entering freely the host cells encountered on the way.

When a sporidium by chance lands on a leaf over a large vein, it enters and develops there. Prevented by the vein from direct downward growth, the mycelium spreads in the tissue between the vein and the upper surface. Such infections show exceptional intracellular growth in the upper epidermis. Plate 4, *D*, represents a bit of such epidermal mycelium drawn from a freehand tangential section of living material.

So far as noted, this mycelium, whether intercellular or intracellular, is haploid in character. A terminal cell about to divide may be momentarily binucleate, but in general the cells are uninucleate.

NUCLEAR DIVISION AND NUCLEAR LOCOMOTION

As a hypha grows apically, the terminal cell elongates, its nucleus divides, and a septum divides this binucleate cell into two uninucleate cells. Division figures of vegetative nuclei are minute. The little that has been learned about mitosis is recorded here:

Plate 5, *A, a*, shows a resting nucleus. It is spherical or ellipsoidal and contains a large central spherical body. It is not certain whether the latter corresponds to the nucleole of higher plants or whether it includes chromatin. In addition, a delicately stained network can sometimes be seen spreading through the nuclear cavity. In *b* is shown what may be a prophase of division. As no detail can be made out in the irregular, dark-stained little mass, no certain identification of the stage is possible. In *c*, is shown what probably is an equatorial plate. The figure is too small to permit a count of the chromosomes. In reproductive areas of this rust (*5*), where division figures are larger, a count shows that the number is ± 5. In *d* is shown an anaphase. Part of the chromosomes have divided and passed to the poles; the rest are still near the equator. In *e*, the chromatin is all at the poles and the two daughter nuclei are connected by a slender strand, which is perhaps the "central spindle." In *f* and *g* the two small daughter nuclei move toward each other, perhaps drawn together by the contraction of the connecting strand. No details of septum formation between the two nuclei have been seen.

EXPLANATORY LEGEND FOR PLATE 4

A.—Intracellular hypha in palisade cell from 6-day infection. × 1,400.
B.—Intracellular hypha in spongy mesophyll cell; 6-day infection. × 1,400.
C.—Intracellular hypha in a bundle-sheath cell; 8-day infection. × 1,400.
D.—Surface view of intracellular mycelium in upper epidermis from 7-day infection located over a vein × 460.
E.—Intercellular mycelium from 6-day infection. × 1,400.

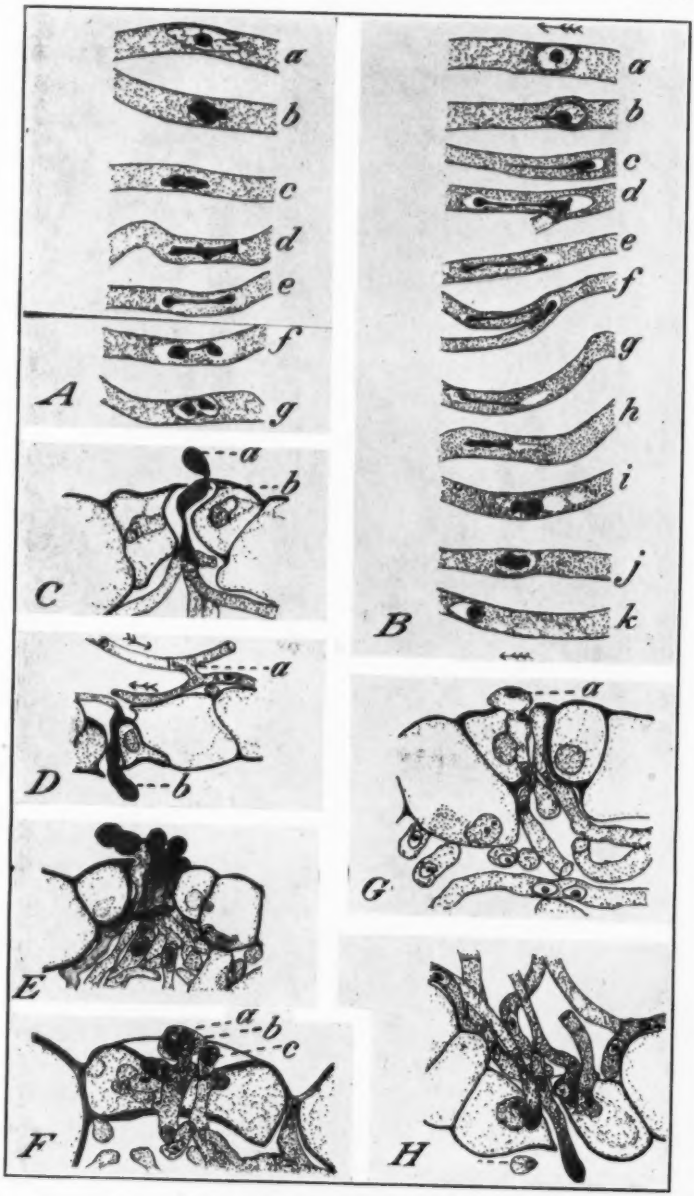
As soon as division is completed, each of the daughter nuclei moves toward the center of its own cell. When a hypha branches, a nucleus moves out into the branch. When an intracellular hypha forms, a nucleus moves into the hypha through the narrow opening in the host cell wall. An older theory assumed that, in this translocation of fungus nuclei incidental to vegetative growth, the streaming of the cytoplasm carried the nuclei along passively. A study of nuclei in actively growing areas throws doubt on this assumption. Moreover, during diploidization fungus nuclei can migrate through hyphae for considerable distances. By no stretch of the imagination can this be thought of as brought about by cytoplasmic streaming. It must be conceded that nuclei possess some form of locomotion.

Nuclear locomotion has been studied in the actively growing tips of hyphae of young haploid vegetative mycelium. Even a casual survey shows that nuclei here vary greatly in shape. Drawings were made representing the full range of variation. A study of these drawings shows that they can be arranged in a sequence that is at least suggestive of the mode of locomotion of the fungus nucleus. In order to make a beginning at understanding nuclear locomotion, the following tentative interpretation is offered.

Plate 5, *B*, *a* to *k*, shows a representative series of nuclear shapes. The arrows indicate the direction of growth of the hypha, i. e., the growing tip of each hypha is at the left of the part drawn. A nucleus in repose (*a*) is spherical or ellipsoidal and is surrounded by undisturbed cytoplasm. Conspicuous within the nucleus is a central spherical body, which, as noted earlier, may be just a nucleole or may include chromatin. In *b* the nucleole has pushed out a slender rod in the direction of the apex of the hypha. This rod stretches the nuclear membrane into a short beak. In *c*, the beak has elongated to a fine tapering hair several times as long as the body of the nucleus. The length of this beak determines the length of the forward stride of the nucleus. In *d* and *e*, material appears to be flowing out from the body of the nucleus into the fine beak. At this stage, the beak is apt to be uneven in diameter, slender in some parts and bulging in others. At *f*, the point of origin of a branch hypha, a nucleus evidently has divided and a septum has formed between the two daughter nuclei. The distal daughter nucleus is now moving on toward the apex of the parent hypha, while the proximal daughter nucleus is moving out into the branch. In *g* and *h*, the evacuation of the old nuclear position is completed, the space being occupied by a rapidly collapsing vacuole, while the elongated rod of nuclear material is contracting into a more compact mass in the new location. It may be that *i* and *j* are later stages in this contraction, while *k* represents the reconstructed nucleus.

EXPLANATORY LEGEND FOR PLATE 5

A.—Stages, *a* to *g*, in mitosis in vegetative hyphae from 6-day infection. × 2,200.
B.—Nuclear shapes, *a* to *k*, found in rapidly growing vegetative hyphae, arranged in a sequence which suggests mode of nuclear locomotion; from 6-day infection. × 2,200.
C.—Stomatal hypha, *a*, *b*, in upper epidermis of 7-day infection. × 1,400.
D.—Detail of lower epidermis of 7-day infection with anastomosis, *a*, and stomatal hypha, *b*. × 1,020.
E.—Hyphae with conidia in stoma of upper epidermis of 8-day infection. × 1,020.
F.—Longitudinal section of stoma with detached conidium at *a*, and young conidia on stomatal hyphae at *b* and *c*; 8-day infection. × 1,400.
G.—Hyphae in stoma of upper epidermis of 8-day infection with conidium at *a*. × 1,400.
H.—Hyphae in stoma of lower epidermis with conidium at *a*; 8-day infection. × 1,400.



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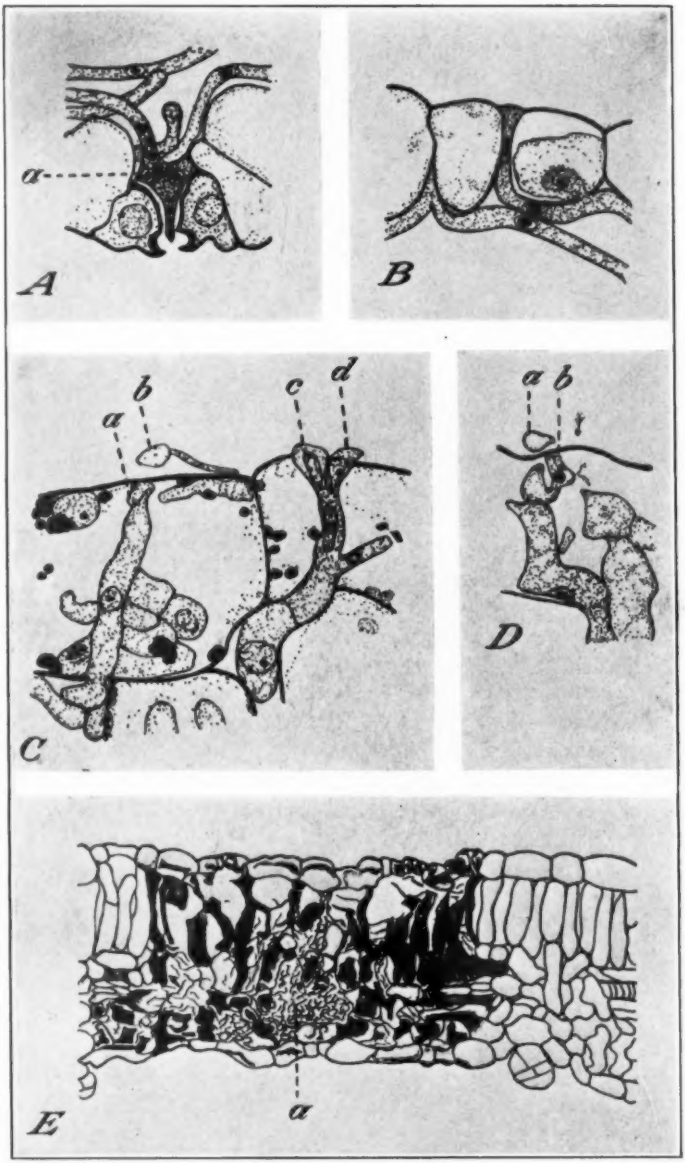

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If the nuclear forms shown in plate 5, *B*, *a*, *b*, and *c*, had been the only ones found, it would have been assumed that the long beak in *c* served as a whiplash and that the nucleus swam ahead by something akin to ciliary motion. Such a hypothesis, however, takes no account of the other nuclear forms.

These various forms of the nucleus are encountered frequently, the majority being represented in every section of an infection. A count of 100 nuclei in the growing tips of hyphae of a 6-day infection and a similar count of 100 nuclei in a 7-day infection gave the results shown in table 1. Nuclei in any stage of mitosis were excluded from the count.

TABLE 1.—*Number of nuclei at each stage of nuclear locomotion among nuclei found in tips of hyphae 100 nuclei each from a 6-day and a 7-day infection of Puccinia malvacearum*

Age of infection (days)	Number of nuclei at indicated stage [1]											Total
	a	*b*	*c*	*d*	*e*	*f*	*g*	*h*	*i*	*j*	*k*	
6	44	7	4	9	4	1	5	8	3	11	4	100
7	53	7	3	10	8	2	3	7	1	5	1	100

[1] See pl. 5, *B*, *a* to *k*, for stages represented by letters.

As will be seen, even in rapidly growing hyphae, about half of the nuclei are in repose, while the rest present one or another of the appearances here interpreted as some stage of locomotion. The stage shown in plate 5, *B*, *c*, is probably more abundant than the tabulated numbers indicate. The long slender beak is easily overlooked and if faintly stained is invisible.

Early workers in rusts saw nuclear figures corresponding to those shown in plate 5, *B*, *d*, *e*, and *h*, and formulated on them the now obsolete theory of amitosis of vegetative fungus nuclei. It is a real question, however, whether any of these nuclear figures may be stages of mitosis. *A*, *b*, supposedly a prophase of division, and *B*, *j*, supposedly a stage of nuclear condensation after a forward stride, are markedly similar. There is much less risk of mistaking any other stage of mitosis for a stage of nuclear locomotion.

SURFACE HYPHAE

Early in the development of vegetative mycelia, hyphae grow to both the upper and the lower surface of the leaf. Hyphae grow into stomatal apertures, grow out through epidermal cells and, more rarely, force a passageway out between epidermal cells.

Almost every infection 1 week old has formed stomatal hyphae. Plate 5, *C*, represents such a hypha emerging through a stoma in the

EXPLANATORY LEGEND FOR PLATE 6

A.—Multinucleate hypha, *a*, in stoma of lower epidermis; 8-day infection. × 1,400.
B.—Hypha reaching surface between cells of upper epidermis of 9-day infection. × 1,400.
C.—Hyphae, *a*, *c*, *d*, growing through cells of upper epidermis to the surface; *c* and *d* bearing conidia; germinating conidium at *b*; 7-day infection. × 1,400.
D.—Conidium at *a* and growth in epidermal cell at *b*, connecting with intracellular hyphae; 8-day infection. × 1,400.
E.—Nine-day infection. Loose aggregation of hyphae at *a*. Both the mycelium and the host cells invaded by it are dead. × 230.

upper epidermis of the leaf, and *D*, *b*, shows an occupied stoma of the lower epidermis. The tips of both of these hyphae are dead. Exposed parts of stomatal hyphae are short-lived, for the closing of the stoma pinches the hypha. The hypha can, however, continue to grow out from its base.

Perhaps successive pinchings as the stoma opens and closes have given these stomatal hyphae their moniliform appearance. Another possibility is that these emergent hyphae are cutting off successive cells in some hitherto unsuspected formation of conidia. Plate 5, *E*, *F*, *G*, *H*, from 8-day infections, also suggests conidial formation. In *E*, several hyphae have grown up through the aperture, forcing the stoma wide open. Each bears a terminal knob, or a chain of small rounded cells. In *F*, which shows a longitudinal section of a stoma, the stomatal hyphae have pushed out stubby little branches, two of which, *b*, *c*, suggest the formation of conidia. Behind one of these hyphae, at *a*, is a small disconnected ovoid spore. *G*, at *a*, again suggests the formation of little ovoid conidia. They vary somewhat in size but are about half the diameter of the sporidia of the rust. In *H*, showing an oblique section through a stoma of the lower epidermis, there are several stomatal hyphae and, at *a*, a spore.

In plate 6, *A*, from the lower epidermis, the outgrowing hypha, *a*, evidently encountered a shut stoma, continued to grow and spread out on the inner face of the stoma, then, when the stoma opened, started to grow down through it. This hypha contains several nuclei. A search was made for free conidia on the surface of the leaf. Only a few have been found but, of course, in fixed material loose cells wash off.

Rarely a mycelial hypha of *Puccinia malvacearum* reaches the surface of the leaf by growing out between ordinary epidermal cells. Plate 6, *B*, shows such a hypha.

Because of the exceptional ability of *Puccinia malvacearum* to grow intracellularly, the hyphae also reach the surface of the host by growing out through epidermal cells (pl. 6, *C*). At *a*, a hypha has grown up to the outer wall of the epidermal cell, and at *c* and *d*, a branching hypha has broken through to the surface. Its shape suggests the formation of conidia. At *b*, is what appears to be a small germinating conidium that has entered the host cell. *D* is more difficult to interpret. At *a* is an empty little cell on the leaf surface, at *b* a small growth inside the host cell in contact with larger hyphae. No connection could be traced between *a* and *b*.

So far as known, *Puccinia malvacearum* produces no spermogonia. The findings recorded above suggest the interesting possibility, however, that this species is developing an accessory spore form by producing little conidia on the scattered hyphae that grow to the surface of the leaf. If what has been seen so far is representative, comparatively few such conidia are formed. There is always the possibility, however, that at a certain age of the fungus, or at a particular time of day or night, or under optimum weather conditions, conidia would be formed more freely.

Knowing that in some species conidia are formed only during the night (*33*), material from plants growing out of doors and from leaves placed in a damp chamber indoors was fixed at intervals during the night. Part of this material was used for freehand sections, and the

rest was embedded in paraffin and sectioned. Only an occasional hint of spore formation has been found. Data up to the present give little encouragement to the idea that conidia are ever formed in abundance.

ORIGIN OF BINUCLEATE CELLS AND FORMATION OF THE SORUS

Under the conditions of these experiments, the growing haploid mycelium reaches the lower epidermis of the leaf sometime between the fifth and the seventh days. By the seventh day the infections show a marked difference in development. In some the mycelium is spreading vigorously, the marginal hyphae are healthy, and the sorus is beginning to form just above the lower epidermis. In others the infection is small, the mycelium scanty, the marginal hyphae and the host cells invaded by them are dying, and there is no young sorus. This difference in development can hardly be explained as due to differences in age or vigor of the host leaf or to varying environmental conditions, for within a millimeter of one of these dying infections in a leaf may be a vigorous mycelium making rapid progress toward spore formation. On the eighth day the difference is more pronounced and by the ninth day after inoculation some infections are dead and others close by are growing rapidly and developing young teliospores. Plate 6, *E*, shows a dead 9-day infection. The fungus had formed a loose aggregation of hyphae at *a*, the place for a sorus, but it failed to shape up for spore formation, and now the hyphae are dead and shrunken. Soon after this, the mycelium disappears and the dead host cells appear clear and empty.

A detailed study was made of twenty 8-day infections from a rather heavily infected leaf. Of these, 16 were growing vigorously and 4 were dying. A section-by-section study shows that the four small dying infections are monosporidial in origin. Only one primary hypha can be found in the upper epidermis adjoining each infection. Moreover, these four are still haploid; their cells are uninucleate. Of the 16 vigorous infections, 14 have 2 or more primary hyphae fairly close together, so that the mycelia developing from them are fully confluent and appear macroscopically as 1 infection, and 2 are obviously double, consisting of 2 tangent infections with only the marginal hyphae interlacing. All of the 16 infections have young sori. In the case of tangent doubles, the sorus is apt to be started between the two infections. If the two infections are so far apart that their mycelia do not meet until after several days' growth, the sorus is correspondingly delayed in starting.

The attempt to make a similar study in 9-day material was only partly successful. The proportion of living and dead mycelia is about the same. In some cases it is still possible to prove the multisporidial origin of the living infections, although primary hyphae have usually deteriorated somewhat by the ninth day; it is, however, no longer possible to identify the primary hypha in the dead infections.

In this experiment the monosporidial infections remained small and haploid, failed to initiate a sorus, and soon died. It is not proved, of course, that under no circumstances would an isolated monosporidial infection develop further.

A closer examination of the young multisporidial infection shows that anastomoses take place between hyphae, both in the vegetative mycelium and at the location for the sorus, and that nuclei move

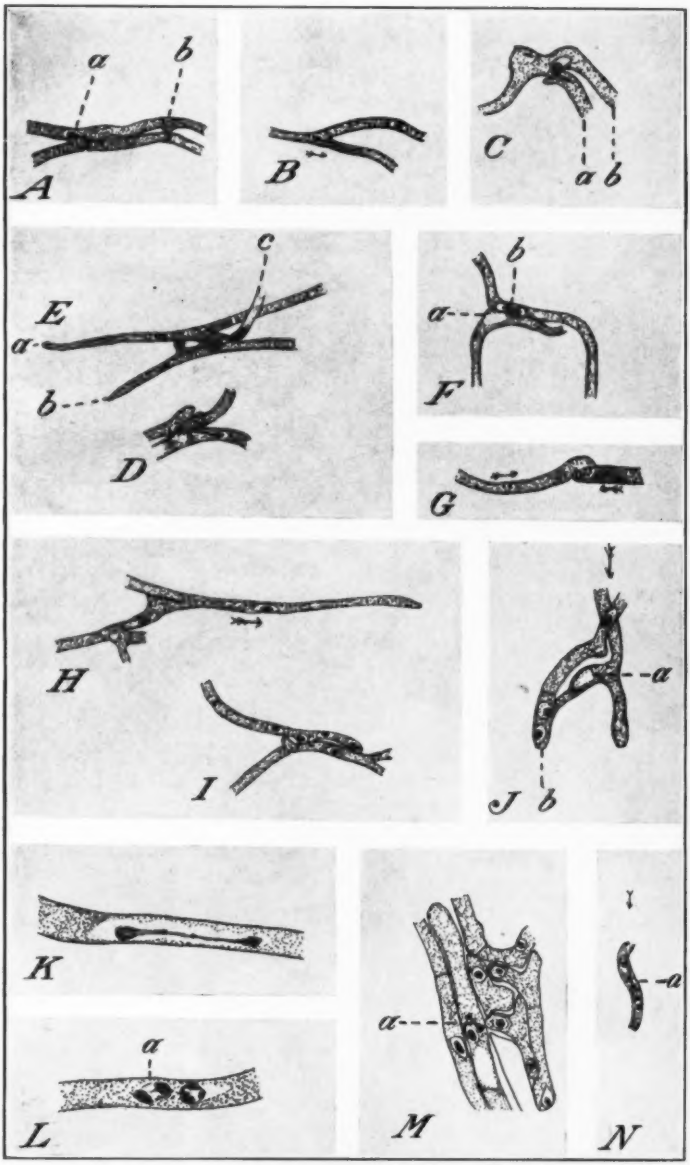
through from one hypha to another. Plate 5, *D*, *a*, and plate 7, *A*, *C*, *D*, *E*, *F*, from 7-day infections, show connections between vegetative hyphae. In plate 5, *D*, at *a*, 2 hyphae growing in opposite directions came close to each other and formed a connecting passageway, giving rise to an H-shape figure. In plate 7, *A*, 2 passageways, at *a* and *b*, formed between parallel hyphae, and a nucleus at *a* is passing over from one hypha to the other. That this is a case of anastomosis and not ordinary branching is seen by comparison with *B*, in which a branch is forming and a nucleus is passing out into the branch. In the one figure there are 4 ends; in the other, 3. In *C* the hypha *a* grew up to and flattened against the hypha *b*; an open passageway formed, and a nucleus is passing through from *b* to *a*. In *D* also, two hyphae are tangent and a nucleus is passing through from one to the other. In *E* two hyphae, *a* and *b*, were growing parallel in the same direction when a third hypha, *c*, grew in and made successive connections with both *a* and *b*. In *F* two hyphae became closely applied to each other. At *a*, in one hypha, is a vacuole; at *b*, in the other hypha, are 2 nuclei. A nucleus may have moved from *a* to *b*.

Plate 7, *G*, *H*, *I*, *J*, from older infections, also shows fusions in vegetative hyphae. Two infections started growth so far apart that they did not meet until they were 8 days old. Neither infection had initiated a sorus. At 8 days of age a few marginal hyphae of one made contact with marginal hyphae of the other. Nearly every one of these contacts resulted in a fusion. *G* is typical of these fusions. The tips of these hyphae met and fused, and the nucleus of one hypha passed over into the other hypha. *H*, from another 8-day preparation, shows an unusual configuration, in which apparently the whole growing tip of one hypha fused with another. In *I* the two hyphae were growing in opposite directions when they met, and there is an aggregation of nuclei near the passageway. In *J* the hypha *a* has contributed its nucleus to *b*.

In infections showing these anastomoses and nuclear transfers, binucleate cells are soon found. No general diploidization of the mycelium takes place. Marginal hyphae, if they are not in actual contact with another mycelium, remain haploid. In the central area, however, cells with more than one nucleus become fairly common. Frequent figures, such as plate 7, *K* (more highly magnified than those preceding), showing nuclear locomotion, and figures such as *L*, *a*; *M*, *a*; *N*, *a*, in which only 1 of the 2 nuclei in a cell is dividing, suggest that the transferred nuclei and their progeny may become distributed along a hypha by successive divisions and migrations.

EXPLANATORY LEGEND FOR PLATE 7

A.—Two hyphae anastomosed at *a* and *b*. Nucleus passing through at *a*. Seven-day infection. × 1,020.
B.—Branching of hypha, from 7-day infection. × 1,020.
C.—Anastomosis of hyphae, *a* and *b*, with nucleus passing through; 7-day infection. × 1,020.
D.—Anastomosis with nucleus passing through; 7-day infection. × 1,020.
E.—Two parallel hyphae, *a* and *b*, with third hypha, *c*, anastomosing with both; 7-day infection. × 1,020.
F.—Anastomosis of two hyphae, with vacuole at *a*, and two nuclei at *b*, from 7-day infection. × 1,020.
G.—Anastomosis between tips of hyphae and transfer of nucleus; 8-day infection. × 1,020.
H.—Lateral union of two hyphae; 8-day infection. × 1,020.
I.—Anastomosis with aggregation of nuclei; 8-day infection. × 1,020.
J.—Anastomosis with transfer of nucleus from *a* to *b*; from 12-day infection. × 1,020.
K.—Migrating nucleus from 7-day infection. × 2,200.
L.—Binucleate cell with only one nucleus, *a*, dividing; from 7-day infection. × 2,200.
M.—One of two nuclei of a cell at *a* dividing; from 7-day infection. × 1,020.
N.—One of two nuclei at *a* dividing; from 8-day infection. × 1,020.



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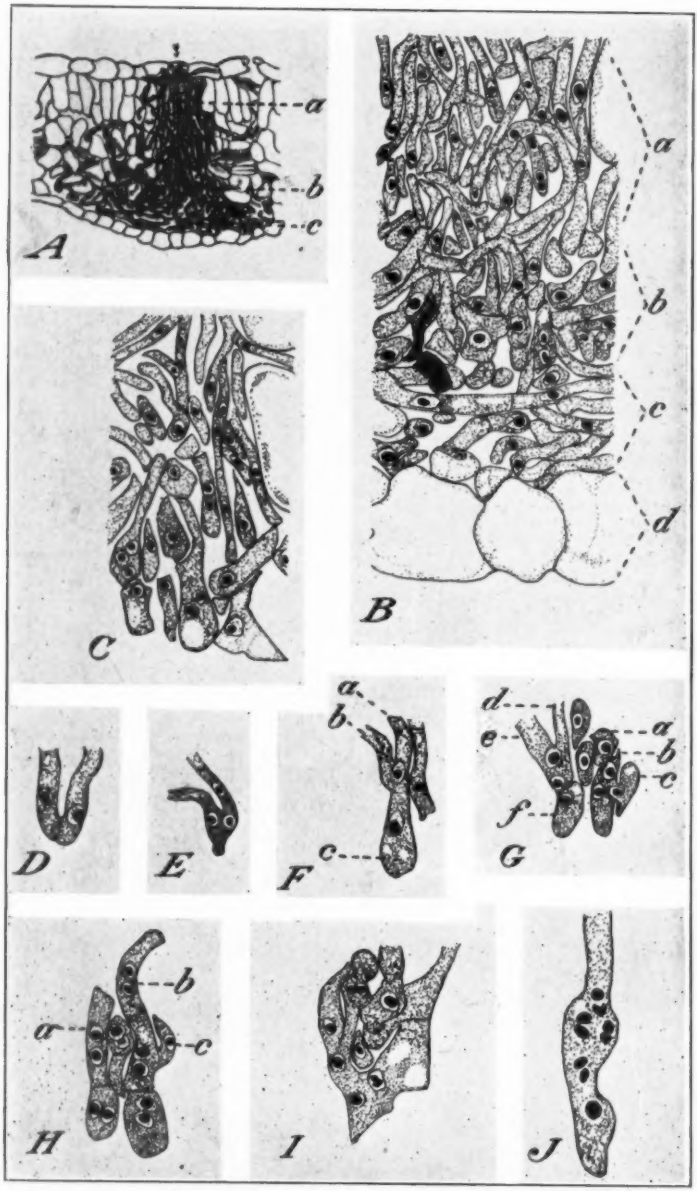

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Plate 8, *A*, represents semidiagrammatically a typical 8-day multisporidial infection. The mycelium first invaded a number of palisade cells at *a* and then grew downward. There is very little lateral spread; the mycelium remains strictly localized. The young sorus is taking shape at *b*. The hyphae nearest the lower epidermis, at *c*, will become the buffer cells and are already somewhat impoverished. As a result of earlier mycelial fusions, some of the hyphae are already diploid when they enter the sporogenous layer. *B* and *C* show enlarged details in which many of the cells contain more than one nucleus. *B*, *a*, shows the mycelium above the sporogenous area; *b*, the sporogenous area; *c*, the buffer cells; and *d*, the lower epidermis.

Other hyphae are haploid when they reach the sporogenous layer and fuse there. Plate 8, *D* to *I*, shows details of fusions in the sporogenous area from 8-day infections. In *D*, two hyphae grew down into the sporogenous layer, and their tips met and flattened against each other. In *E*, the wall between the two is dissolved. In *F*, two hyphae, *a* and *b*, grew down, met, and joined, and the fusion cell grew on to *c*. Figures such as this are common. Sometimes the fusions are more irregular. In *G*, apparently 3 cells, *a*, *b*, and *c*, fused; the combination possesses 4 nuclei. Two hyphae, *d* and *e*, fused and grew on downward. Whether *f* represents a cell being cut off or a further fusion is not clear. In *H*, the hyphae *a* and *b* were diploid before reaching the sporogenous layer, but *b*, none the less, has been joined by a third hypha, *c*. In *I*, the connections and fusions are so complicated that several nuclei occur within the limits of the fusion cell. Multinucleate cells in the sporogenous area are not rare; *J* represents an extreme example.

In 9-day infections (if fusions have not been delayed by too great a distance between the component infections) the sorus is larger and young teliospores are forming. Hyphae resulting from earlier mycelial fusions (pl. 9, *A*) can form spores directly. In *C* the one terminal cell of the main hypha, *b*, will become one spore, while a side branch, *a*, will later give rise to another.

Fusion cells (pl. 8, *F*), so abundant in 8-day material, have continued to grow, giving rise to cells such as that shown in plate 9, *B*. At this stage it still is occasionally possible to trace the early history. The two hyphae of plate 9, *B*, *a* and *b*, fused at *c* and the fusion cell grew on to *d*. Usually the fusion cell contains two nuclei, but irregularities are common. Here (*B*) there are two full-grown nuclei plus a pair of small, newly divided nuclei. In *D* appearances suggest that two hyphae, *a* and *b*, met, fused, and then, by adjusted divisions and growth, gave rise to two hyphae, *c* and *d*, both composed of binucleate cells.

Soon after this stage the part of the sorus above the spores becomes a dense pseudoparenchyma (pl. 9, *F*), and it is seldom possible to

EXPLANATORY LEGEND FOR PLATE 8

A.—Diagram of 8-day fertile infection showing invaded palisade cells at *a*, sporogenous area at *b*, and buffer cells at *c*. × 160.

B.—Detail of 8-day fertile infection showing central mycelium, *a*; sporogenous area, *b*; buffer cells, *c*; and lower epidermis, *d*. × 1,020.

C.—Detail from 8-day fertile infection showing cells with more than one nucleus in and above the sporogenous area. × 1,020.

D to *I*.—Details from sporogenous area of 8-day infections. *D*, Two hyphae meeting at tips and about to fuse. *E*, Newly fused hyphae. *F*, Hyphae *a* and *b* fused and the fusion cell grew down to *c*. *G*, Hyphae *a*, *b*, *c*, fused; *d* and *e* fused; *f* may be a further fusion. *H*, Hyphae *a* and *b* already diploid but *b* is joined by *c*. *I*, Much-involved fusions. × 1,020.

J Multinucleate cell at sporogenous area; 8-day infection. × 2,200.

trace the origin of the spore-bearing cells in this mass of tightly interwoven hyphae. *E* shows a detail from a 12-day sorus. As new spores continue to form for some time, several stages of spore development can be found side by side. The appearance of a small 15-day open sorus is shown semidiagrammatically in *F*.

Cytological details of the development of the teliospore, the nuclear fusions at maturity, the germination of the spore, the reduction divisions, and the formation of the sporidia are presented in another paper (*5*) and are not repeated here.

DISCUSSION

It has been assumed that a short-cycle rust without spermogonia, like *Puccinia malvacearum*, is without means of crossing. A closer view of the situation makes this assumption doubtful.

Under natural field conditions, the infections of *Puccinia malvacearum* on a leaf are not all of the same age. As soon as one infection matures its teliospores germinate (weather permitting), and continual crops of sporidia are formed and freed. When a sporidium drops upon a leaf it is apt to roll down into a furrow. Hollyhock and mallow leaves are not smooth; they are rather deeply creased and furrowed at the veins. Sporidia accumulate in these creases and can be seen there by dozens. After a few hours in damp air, the wholesale entrance of these sporidia into epidermal cells can be found. The resulting mycelia are crowded and interlace freely. Moreover, mallow and hollyhock leaves are regularly visited by small spiders and insects; in fact, it is rare to find an infected leaf in the field that is free from such visitors. These help to carry sporidia about.

There are indications, too, that immature infections, too young to be bearing teliospores, can produce small conidia on the scattered hyphae that reach the surface of the leaf by growing into stomatal apertures or growing out through epidermal cells. Only a few such conidia have been found. There is, of course, the possibility that under the right conditions such spores would be formed in greater abundance, but material taken at different times of day and night from plants in ordinary air and in damp chambers, lends small encouragement to such a belief. There is a little evidence that these conidia can germinate and enter the host leaf.

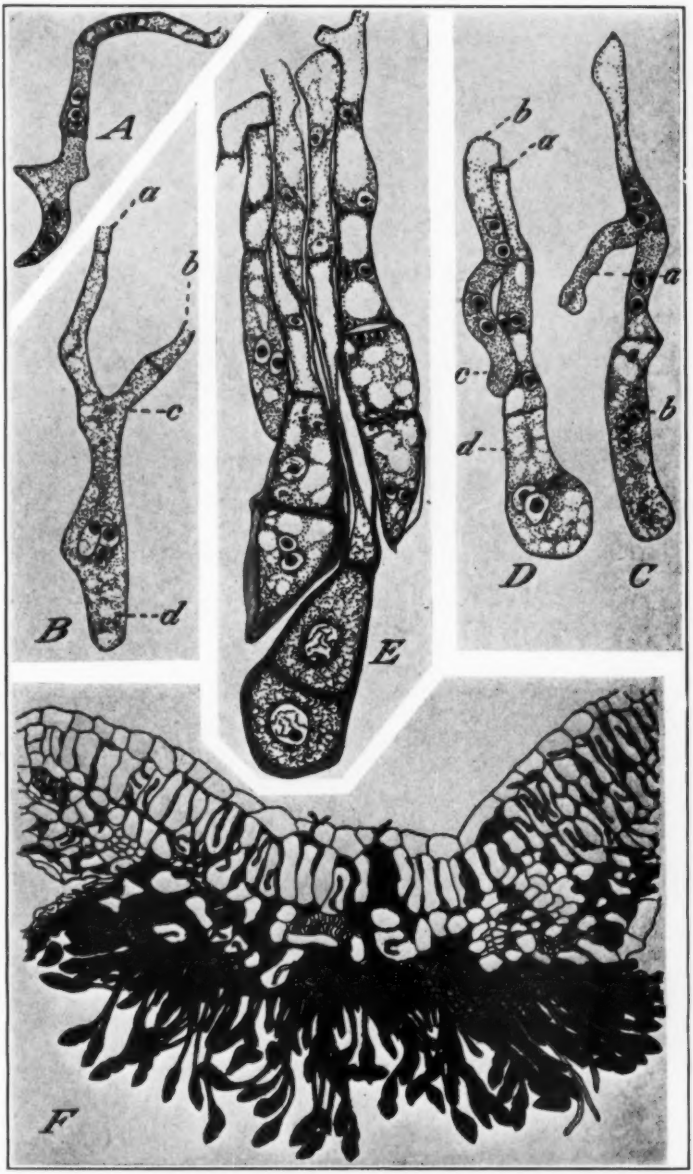
The formation of even a few such conidia early in the development of an individual might be of significance, for they could easily be transferred by wind or by insects, and if by chance placed near another infection, might grow in and make contact with it.

Even in a rust without spermogonia, then, there are frequent contacts between individuals. The means of crossing exist.

This formation of a few scattered conidia in *Puccinia malvacearum* that, theoretically at least, could help to replace in function the absent spermatia, is not unique among higher fungi. De Bary

EXPLANATORY LEGEND FOR PLATE 9

A.—Hypha with trinucleate cells from sporogenous area of 9-day infection. × 1,020.
B.—Hyphae *a* and *b* fused at *c* and grew to *d*. Irregular nuclear content. From sporogenous area of 9-day infection. × 1,020.
C.—Diploid hypha branching. Both *a* and *b* will give rise to teliospores. Nine-day infection. × 1,020.
D.—Hyphae *a* and *b* fused and then both grew on as diploid hyphae, *c* and *d*; 9-day infection. × 1,020.
E.—Detail of 12-day infection with growing teliospores of different ages. × 1,020.
F.—Diagram of small 15-day open sorus. × 160.



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(*14*), in 1887, cites several cases of "doubtful spermatia" in Ascomycetes, and Backus (*13*) has summed up a variety of irregularities and doubtful cases reported in recent literature. The ability of fungi to produce conidia at unexpected times and places is further illustrated by the production in the diplophase of *Pholiota* (*27*) of several accessory spore forms of a conidial nature.

In a rust with spermogonia that produce thousands of spermatia in a liquid attractive to insects, there is abundant opportunity for the transfer of cells from one infection to another. A subsidiary spore form like these conidia, under such conditions, would seem to be of less biologic importance to the rust. A hint that such conidia may be formed, however, is given by Rice (*30*), who mentions and figures, without comment, the occurrence of small "spheres" attached to or lying close to the stomatal hyphae in corn rust.

Hyphae growing out to the leaf surface in young haploid infections of rusts have been known since the days of De Bary (*14, p. 278*) and have been noted frequently since then (*1, 2, 3, 4, 6, 8, 10, 11, 30*). The only rust investigated recently in which surface hyphae have not been found is flax rust (*7*). Further studies may bring to light more cases in which such surface hyphae function as conidiophores.

There is evidence that the isolated monosporidial infection of *Puccinia malvacearum* tends to be retarded in development, remains minute, and under some conditions, at least, remains haploid and dies young without forming a sorus. With the limited data presented here, however, it cannot be taken for granted that an isolated infection never develops a sorus. With other strains of the rust, or other hosts, or other culture conditions, it is possible that a sorus could be formed in an isolated monosporidial infection. Ashworth (*12*) reports that, in 18 out of 1,000 (i. e., 1.8 percent) single-spore inoculations of *P. malvacearum*, infection took place and sori developed. She assumed that infection did not take place in the other 982 inoculations. So far as stated, however, these were not sectioned, and it is possible that many of the inoculations resulted in minute infections that died without becoming large enough to be visible macroscopically. It is also possible that, while the 18 inoculations resulting in infections with sori were still small, insects transferred conidia or sporidia to them. On this basis, *P. malvacearum* would be heterothallic.

When two mycelia of *Puccinia malvacearum* meet within the leaf, anastomoses form freely. Anastomoses between hyphae of the same mycelium or of two overlapping mycelia of the same species are common in the higher fungi. In species of Hymenomycetes that can be grown in Petri dishes, it is comparatively easy to find such anastomoses (*17*). It long has been believed that, in rusts also, two mycelia in contact form connections and that nuclei pass through these connections, resulting in the diploidization of both components. Demonstration of this in rusts is difficult, for hyphae wind about in the irregular air spaces of the leaf and in sectioned material appear as comparatively short pieces.

Indirect but none the less conclusive proof of anastomoses in rusts is given by Brown (*16*). Sporophytic (uredial) and haploid mycelia of *Puccinia helianthi* Schw. were grown side by side on the same leaf. The diploid mycelium contributed to the haploid mycelium nuclei of the kind it lacked and the latter at once developed normal aecia.

In *Puccinia malvacearum*, anastomoses between mycelia are abundant and fairly conspicuous. When two primary hyphae are close together and the first mycelial growth is fairly dense, it is hard to trace connections between the two, although the early presence of binucleate cells in such mycelium suggests that cell fusions have occurred. But when 2 mycelia are farther apart and the first contacts are made between scattered marginal hyphae that have grown toward each other from the 2 infections, nearly every meeting point shows anastomosis.

The presence of anastomoses is not in itself proof that fertilization is taking place. Buller (*17*) has shown that in *Coprinus* a number of adjoining mycelia may unite into a compound mycelium, forming an intimate network with thousands of connections. This can take place equally well whether the species is homothallic or heterothallic. Combining is of advantage in the absorption and transportation of food materials for the building of a fruit body. Moreover, this type of combination takes place quite independently of sex. Buller says (*17, pp. 185–186*):

> From these observations we are justified in concluding that, in *Coprinus lagopus* and similar Hymenomycetes, any two like mycelia or any two unlike mycelia can unite with one another to form a compound mycelium and that, in general, any one kind of mycelium at one and the same time can combine with any number of other mycelia with which it may come into contact, whatever may be their sexual condition. [He adds, however]: If two mycelia which do not react sexually happen to unite, no association takes place between their nuclei; but, if two mycelia of opposite sex happen to unite, then through the openings made by the first few hyphal fusions nuclei pass from one mycelium into the other mycelium, conjugate pairs of nuclei are soon established in both mycelia, and the mycelial haplophase quickly changes into the diplophase.

In *Puccinia malvacearum*, anastomoses between mycelia are accompanied by the transfer of nuclei. It is not uncommon to find a nucleus in the act of passing through an anastomosis from one hypha to the other. Moreover, shortly after these anastomoses and nuclear transfers, binucleate cells are to be found in the mycelium and a sorus starts promptly. So far as these details also are concerned, it might be supposed that *P. malvacearum* is heterothallic and that this is an ordinary diploidization process.

One further item should be taken into account, however. In heterothallic fungi with 2 sex groups (or compatibility groups, as some writers prefer to call them), roughly 50 percent of the matings are between individuals of the same group and remain sterile, while the other 50 percent are between opposite groups and lead to fertilization and the diploid generation. Present data on *Puccinia malvacearum* are too limited to be conclusive, but, so far as they go, they indicate that all matings lead to cell fusions and the development of a sorus. This recalls the 100-percent interfertility between "geographic" strains in certain Hymenomycetes (*23, 25, 31*).

Since rusts are obligate parasites and it is not feasible to subdivide infections and plant bits of them in pairs in all possible matings, a genetical analysis cannot be made. Without it, no certain conclusions can be drawn.

It is possible to look at the above data from quite a different point of view. Suppose for the moment that *Puccinia malvacearum* is homothallic. The young sporidium of *P. malvacearum* is uninucleate.

As the spore matures this nucleus regularly divides once. Suppose that as the result of this division one daughter nucleus in the sporidium is (+) and the other (−). Reference to plates 1 and 2 show that both nuclei of a sporidium move into the host and are soon located in separate cells of the primary hypha. Each of these cells gives rise to uninucleate mycelium. On this assumption every monosporidial mycelium would consist of mingled (+) and (−) hyphae in approximately equal numbers. Suppose further that (+) and (−) hyphae grown from the same sporidium react but feebly with each other and in many cases no pairing at all takes place and the mycelium dies without producing a sorus. In a few there is further development and the formation of a sorus. When, on the contrary, two of these monosporidial infections meet within the leaf, anastomoses form, there is an active interchange of (+) and (−) nuclei, and the (+) nuclei of each mycelium meet (−) nuclei of the other. Pairing of nuclei and diploidization can now progress rapidly and a sorus forms in all cases. Of course this theory has not been and perhaps cannot be proved. Its only justification is that it covers the observed facts.

Puccinia malvacearum is a rust with a reduced life cycle, maintaining itself by repeating telial generations. At the time when the other spore forms were lost from the cycle, survival depended on the immediate development of some substitute method of attaining the binucleate phase. Sexual reproduction here is reduced to the simplest terms. There is a complete absence of sex organs and gametes. As in the Hymenomycetes, vegetative hyphae can anastomose and serve as the channel for the interchange of nuclei. Reproduction here is concerned fundamentally with the pairing of nuclei. Gametes can be dispensed with, but the irreducible minimum for sexual reproduction is the presence of two kinds of nuclei, whether the difference between them is labeled a sex factor, compatibility factor, or self-sterility factor (*9*, *19*, *20*, *21*, *22*).

Evidence has accumulated in recent years that the nuclei of higher fungi can migrate freely through a mycelium and even pass through anastomoses from one mycelium to another. Buller (*17*) has proved that nuclei introduced at one point into a haploid mycelium of *Coprinus* multiply and become rapidly dispersed throughout the whole mycelium. That nuclei of rusts have the same power of locomotion is shown by *Puccinia sorghi* Schw. (*8*), in which 24 hours after spermatization 60 percent of the cells throughout the mycelium contain more than one nucleus.

The mode of locomotion of a fungus nucleus is unknown. As a beginning toward clearing up this obscure point, the different shapes of nuclei found in rapidly growing tips of hyphae have been arranged in a sequence that can be interpreted as stages in the forward stride of a nucleus. According to this series, a nucleus pushes out a long slender beak, then flows forward into the beak and condenses in the new position, leaving a temporary vacuole in the cytoplasm behind it. This is somewhat in the manner of amoeboid motion. The extreme slenderness of the initial beak helps to explain how a nucleus could pass through a very fine pore in a septum when moving from one cell of a hypha to the next. Buller (*17*) has figured out the rate at which *Coprinus* nuclei travel when diploidizing a haploid mycelium. A nucleus at full speed moves ahead a distance equal to its own diam-

eter every 6 seconds. In *Puccinia malvacearum*, the beak on a nucleus in motion becomes about three times as long as the body of the nucleus, and the length of the beak determines the length of the forward stride. If a rust nucleus can travel as fast as a *Coprinus* nucleus, a single stride would take about 18 seconds. If one allows for a pause between strides (table 1), the advance itself must take less than 18 seconds.

In *Puccinia sorghi*, fertilization is followed by wide-spread diploidization of the mycelium. In *P. malvacearum* binucleate cells are found principally in the neighborhood of the sorus. The cells of marginal hyphae, except when in direct contact with another mycelium, remain uninucleate. Correlated with this difference between the two species is the fact that one mycelium of *P. sorghi* produces many aecia in successive marginal circles, while *P. malvacearum* produces only one central sorus.

SUMMARY

Puccinia malvacearum Bert. is a short-cycle rust of hollyhocks and mallows maintaining itself by repeated telial generations. Spermogonia, aecia, and uredia are unknown.

Teliospores can germinate as soon as formed, giving rise to a promycelium bearing four binucleate sporidia. The sporidia germinate at once and their germ tubes enter the leaf and give rise to uninucleate mycelium, which is both intercellular and intracellular.

Nuclear locomotion incidental to vegetative growth and also the longer nuclear migrations during diploidization have been studied. In making a forward stride, a nucleus pushes out a long slender beak, then flows forward into the beak and condenses in the new position, leaving a temporary vacuole in the cytoplasm behind it.

Hyphae reach both the upper and the lower surface of the host leaf by growing into stomata and by growing out through and, more rarely, between the other epidermal cells. There is some evidence that these surface hyphae produce small ovoid conidia about half the size of sporidia.

The isolated monosporidial infection is retarded in growth and may die without developing a sorus.

Whenever two monosporidial mycelia meet within the leaf anastomoses form and a nuclear interchange takes place, followed by localized diploidization and the development of a sorus. Some hyphae are already diploid when they reach the sporogenous area of the sorus and can give rise directly to teliospores. Others are haploid and pair in the sorus before forming teliospores.

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PHYSIOLOGIC SPECIALIZATION OF MELAMPSORA LINI ON LINUM USITATISSIMUM [1]

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INTRODUCTION

Melampsora lini (Pers.) Lév., the fungus that causes rust of cultivated flax, *Linum usitatissimum* L., occurs in all the major seed flax- and fiber-flax-producing areas of the world. Injury to the seed crop results from a reduction in the amount of foliage and from the utilization by the fungus of some of the food of the host plant. In addition to interfering with the normal photosynthetic metabolism of the host plant, rust on fiber flax injures the quality by causing breakage of fibers and preventing normal retting, thus producing what is known as "measly" fibers (*23*).[3] Consequently a small amount of infection may injure the quality of a fiber-flax crop, while it is only under epidemic conditions that the rust may be destructive to seed flax. Only occasionally is flax rust very destructive in Minnesota and the Dakotas, where most of the domestic flaxseed is grown. However, it sometimes occurs in epidemic form in these areas, and Brentzel [4] and Hart (*9*) have reported losses ranging from a trace to 100 percent.

Measures that have been recommended for the control of flax rust include early sowing, thorough cleaning of the seed, crop rotation, use of high, well-drained land, destruction or removal of infected straw, and the use of resistant varieties. Henry (*10*) considered the last-named method the most promising and found rust immunity to be inherited independently of morphologic type or wilt resistance.

In a program to develop disease-resistant varieties of crop plants it is essential to know whether more than one physiologic form of the pathogen occurs and, if so, the varietal host range, distribution, and stability of each form. The object of the investigation herein reported was to obtain this information in regard to *Melampsora lini*.

HISTORICAL REVIEW

Persoon (*18*) described a rust fungus on *Linum catharticum* L. and *L. usitatissimum* in 1801 and named it *Uredo miniata β lini*. In 1847 Léveillé (*15*) transferred it to the genus *Melampsora*, calling it *M. lini*. Buchheim (*5*) states that Körnicke, in 1865, decided that the rust on cultivated flax, *L. usitatissimum*, was physiologically

[1] Received for publication July 26, 1935; issued January 1936. Cooperative investigations between the North Dakota Agricultural Experiment Station and the Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture.

[2] The writer is indebted to M. N. Levine, pathologist, H. B. Humphrey, principal pathologist, and A. G. Johnson, principal pathologist, Division of Cereal Crops and Diseases, Bureau of Plant Industry, U. S. Department of Agriculture, for criticism of this manuscript; to A. C. Dillman, associate agronomist, Division of Cereal Crops and Diseases, for a tentative classification of the varieties of flax and for supplying seed; and to H. L. Bolley and T. E. Stoa, of the North Dakota Agricultural Experiment Station, and C. C. Allison, of the Minnesota Agricultural Experiment Station, for supplying flaxseed.

[3] Reference is made by number (italic) to Literature Cited, p. 836.

[4] FROMME, F. D. RUST CAUSED BY MELAMPSORA LINI (PERS.) DESM. U. S. Dept. Agr., Bur. Plant Indus. Plant Disease Bull. Sup. 15: 168–169, illus. 1921. [Mimeographed.]

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distinct from that on *L. catharticum*, and called the former *M. lini* var. *liniperda*. Since then the host range of rusts occurring on different species of *Linum* has been studied by a number of investigators. Fuckel (*8*), Palm (*17*), and Buchheim (*5*) concluded from cross-inoculation studies that rust on cultivated flax was physiologically and, in some cases, morphologically distinct from that on certain wild flaxes. Arthur (*2*), in demonstrating that *M. lini* was eu-autoecious, obtained pycnia and aecia on *L. lewisii* Pursh and *L. usitatissimum* by inoculation with teliospores produced on the latter species. Hart (*9*) was unable, however, to infect *L. lewisii* with urediospores from *L. usitatissimum* but did secure successful infection of *L. rigidum* Pursh. Lafferty, Rhynehart, and Pethybridge (*14*) obtained slight but abnormal infection of *L. angustifolium* Huds. with urediospores from *L. usitatissimum*. Henry (*11*) found that certain strains of *L. usitatissimum*, *L. angustifolium*, *L. usitatissimum* var. *crepitans* Bönningh., *L. rigidum*, and *L. sulcatum* Riddell were completely susceptible to *M. lini* collected on *L. usitatissimum*, and that certain strains of *L. usitatissimum* and *L. angustifolium*, as well as all tested strains of *L. perenne* L., *L. austriacum* L., *L. grandiflorum* Desf., *L. flavum* L., and *L. catharticum*, were immune.

Hart (*9*) obtained urediospore collections of *Melampsora lini* on *Linum usitatissimum* from a number of localities in the United States and Canada but could not demonstrate the occurrence of physiologic forms from their reactions on a susceptible and an immune variety of cultivated flax. Henry (*10*) suspected the occurrence of physiologic forms of rust on cultivated flax but did not demonstrate their existence. He found that four strains of flax that had been selected by Dorst (*7*) for their resistance to rust in the Netherlands were uniformly susceptible when grown in Minnesota.

MATERIAL AND METHODS

RUST COLLECTIONS AND INOCULATION PROCEDURE

The rust collections used in these studies were made in the field in 1931, 1932, 1933, and 1934. Because of drought, rust was of little economic importance during this period in the flaxseed-producing area of the United States, but a scattered infection occurred throughout Minnesota and the eastern parts of North Dakota and South Dakota. The pathogenicity of 99 uredial collections was studied during these 4 years. Most of the field collections contained but a few uredia and each collection was increased on a susceptible variety in the greenhouse. The urediospores thus obtained were collected in glass vials and stored at 4° C., at which temperature they retained their viability from 2 to 4 months. Pathogenicity tests were made by inoculating approximately twelve 30-day-old plants of each variety with the increased supply of urediospores by dusting the spores from a camel's-hair brush onto the leaves and terminal bud. The inoculated plants were placed in moist chambers for 24 hours at a temperature of 14° to 16° C. and sprayed periodically with an atomizer. They were then removed to rust compartments in a greenhouse kept at a temperature of approximately 20° C. During the winter months a light day of 16 hours was maintained by supplementing daylight with artificial illumination. Final readings were made 10 to 15 days after inoculation, depending on the effect on pustule formation of temperature and light conditions during the period of incubation.

DIFFERENTIAL HOSTS

Although the existence of physiologic forms of *Melampsora lini* on common flax had been suspected by Henry (*10*) prior to the present studies, it had not been proved nor had suitable differential hosts been discovered. The work of previous investigators on physiologic specialization in the rusts and other fungi had indicated that differential hosts most likely would be obtained from resistant varieties and those possessing diverse morphologic characters. In trying to discover potential differentials, the reaction of 50 varieties of flax to the 36 rust collections made in 1931 and 1932 was studied. These varieties had been chosen because they represented diverse morphologic types or had been reported as resistant to rust.

In these tests it was discovered that many varieties reported as resistant in field trials showed no resistance in greenhouse inoculation tests. Furthermore, the reaction of individual plants of varieties possessing some resistance was extremely variable. Consequently, it was necessary to develop lines pure for rust reaction from those varieties that gave indications of possessing differential potentialities. This was accomplished by plant selection. It was found, for example, that two-thirds of the plants of Williston Golden (C. I.[5] 25) showed a high degree of resistance when inoculated with form 1, and that the remaining third showed extreme susceptibility. All plants of this variety were susceptible to form 2. Those plants that showed resistance to form 1 were grown to maturity in the greenhouse, and seed from each plant was increased in the field nursery. The progeny of each plant selection was harvested separately and tested for rust reaction to form 1. Many of the progenies thus obtained continued to segregate for resistance and susceptibility, but several were found to be pure for resistance. One of the latter was subsequently selected as a differential strain for future work. Similarly, it was found that 90 percent of the plants of Buda (C. I. 270) were resistant to form 1, while all plants of this variety were susceptible to form 4. A strain of this variety that was pure for resistance to form 1 was developed by the method used in obtaining the resistant strain of Williston Golden.

The reaction of the differential strains of Williston Golden and Buda to the 36 collections made in 1931 and 1932 indicated that at least 5 physiologic forms of flax rust were present. Monosporous uredial cultures were obtained from each of the 5 forms that appeared to be physiologically distinct. In every instance the pathogenicity of the monosporous culture was identical with that of the original collection. The pathogenicity of these 5 monosporously derived forms to 115 additional varieties was determined in 1932. By these tests and the subsequent increase of certain plant selections, a line pure for rust reaction was obtained from each of 12 additional varieties of flax possessing differential potentialities. Four of these, Samarkan (C. I. 514), Abyssinian (C. I. 511), and Akmolinsk (C. I. 515 and 520), although varying somewhat in the degree of susceptibility, reacted similarly to the different forms. Another strain of Abyssinian (C. I. 701) was resistant to the same forms as were the varieties mentioned above but was also resistant to some of the rust forms to which these varieties were susceptible. Selections from Redwing (C. I. 499) possessed varying degrees of resistance but reacted in general as did the differential strain from Buda. The selection from the fiber flax, J. W. S.

[5] C. I. refers to accession number of the Division of Cereal Crops and Diseases.

(C. I. 708), was either highly resistant or very susceptible to the different forms. The selection from Argentine (C. I. 705) was particularly sensitive to changes in light conditions. This change in reaction was especially noticeable in those forms to which this selection was more or less resistant. The number and size of pustules and the abundance of spores in the pustules were greater in clear weather than in cloudy weather. However, the change in reaction was not sufficient to nullify the value of this variety as a differential. The selections from Diadem (C. I. 321), "very pale blue crimped" (C. I. 647), and Williston Brown (C. I. 803), a brown-seeded selection, probably a hybrid or a mixture, found in a sample of Williston Golden (C. I. 25), were susceptible to most forms of rust but were sufficiently resistant to other forms to be of value as differentials. The selection from Kenya (C. I. 709) was resistant to most forms but semiresistant to some.

HOST REACTION AND TYPES OF INFECTION

The classes of host reaction and infection types used by Stakman and Levine (*20*) served as a guide for formulating the classification used in these studies. Apparently, flax varieties give more diverse manifestations of resistance to rust infection than do wheat varieties, and the classification of host reaction was modified accordingly. The principal types of reaction of flax varieties to rust infection are described below and shown in plate 1.

Classes of host reaction		*Types of rust infection*
Nearly immune	(0)	No uredia developed; hypersensitive flecks or necrotic lesions usually present, but sometimes there is no evidence of infection.
Resistant	(1)	Uredia minute to small, rarely extending through the leaf, usually distinct and scattered in chlorotic to necrotic areas, but in some cases pustule formation is not accompanied by either chlorosis or necrosis of the surrounding leaf tissue.
	(2)	Uredia small to medium, associated with distinct necrosis of the leaf; may be scattered or may form crustlike aggregations in necrotic areas; if isolated, usually are surrounded by a necrotic zone.
Semiresistant	(3—)	Uredia variable; heavily inoculated areas necrotic, with arrested pustule development; medium to large pustules produced in healthy tissue adjacent to necrotic areas; pustules on stem and cotyledons small but with no evidence of hypersensitiveness.
Moderately susceptible	(3)	Uredia medium to large; well developed but not compound; usually extending through the leaf to both surfaces; development somewhat retarded in heavily infected portions of the leaves; tissues adjacent to uredia may become more or less chlorotic as the pustules mature.
Highly susceptible	(4)	Uredia large and, if isolated, usually compound, extending through leaf to both surfaces; at first leaves show little chlorosis but later may become chlorotic and die prematurely.

Hard and fast rules for pustule classification cannot be followed. The types of infection exhibited by a variety depend upon such factors as light intensity, length of day, temperature, and age and vigor of the host plant, as well as upon the pathogenic properties of the rust form involved. All ranges of reaction between immunity and complete susceptibility occur, and whether the borderline cases fall into one type of host reaction or into another often depends upon the arbitrary judgment of the observer.

There appear to be at least two distinct forms of resistance in flax. In some varieties resistance is manifested by a reduction in the size of the individual uredia, together with more or less chlorosis, and the eventual premature death of the infected areas of the leaf. In other varieties resistance is manifested by necrosis of the infected region, coupled with more or less repressed pustule formation. Varieties with host reactions of type 1 show different degrees of the first form of resistance; those with reactions of type 2, different degrees of the second form. The extreme cases of both kinds of resistance would fall in the group having reactions of type 0, in which chlorosis or necrosis of the infected portions of the leaves occurs without pustule formation. Reactions of type 1— include those in which chlorosis of the infected leaves occurs but in which the minute uredia do not break through the epidermis; reactions of type 1 include those in which the small uredia, usually borne in chlorotic areas of the leaves, break through the epidermis; and reactions of type 1+ include those in which small, erumpent uredia are produced, with but slight, if any, chlorosis of the surrounding leaf tissue. Reactions of type 2— are characterized by the production of small aggregations of rudimentary uredia in necrotic areas of the leaves; those of type 2, by the production of small to mid-sized uredia surrounded by a sharp necrotic zone; and those of type 2+, by a crustlike structure resulting from the aggregation of uredia produced in necrotic areas of the leaf. Each form of resistance, as represented by types 1 and 2, covers a range of host reaction extending from near immunity to the borderline of susceptibility. Consequently, one form parallels the other in degree of resistance and neither can be considered, in this respect, subordinate to the other.

No cases of a truly mesothetic type of rust infection, comparable to those occurring in wheat (*20*), oats (*3*), and rye (*6*), were observed on flax. However, there were cases on the borderline of resistance and susceptibility in which monosporous rust cultures produced both necrosis and normal uredia. Since these uredia were well developed and not always produced in or surrounded by necrotic areas, infections of this type were classified as the 3— type and the varietal reaction as semiresistant.

EXPERIMENTAL RESULTS

DIFFERENTIATION OF PHYSIOLOGIC FORMS

Fourteen physiologic forms of *Melampsora lini* infecting *Linum usitatissimum* have been differentiated by the use of seven varieties of cultivated flax. With the study of additional rust collections and the discovery and purification of still other differential varieties, it is probable that more forms will be distinguished. Tests already conducted indicated that additional forms may have been present in the 99 rust collections studied. It was thought inadvisable, however, to establish new forms based on these minor differences, even though they were consistently obtained.

These 14 physiologic forms have been differentiated by the reaction of the selected strain from each of the seven varieties used in the following key. The reactions of each of these seven varieties are given in table 1. In this table the reactions of two additional varieties also are given for additional information and for possible use in differentiating forms not yet studied.

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KEY

Buda resistant.
  Williston Golden resistant.
    Akmolinsk resistant.
      Williston Brown semiresistant to resistant ..... Form 10
      Williston Brown susceptible ..... Form 1
    Akmolinsk susceptible.
      J. W. S. resistant ..... Form 5
      J. W. S. susceptible ..... Form 7
  Williston Golden susceptible.
    "Very pale blue crimped" resistant ..... Form 11
    "Very pale blue crimped" susceptible ..... Form 6
Buda semiresistant.
  Williston Golden resistant ..... Form 3
  Williston Golden susceptible ..... Form 14
Buda susceptible.
  Williston Golden resistant.
    Akmolinsk resistant.
      J. W. S. resistant.
        Kenya resistant ..... Form 4
        Kenya semiresistant ..... Form 12
      J. W. S. susceptible ..... Form 13
    Akmolinsk susceptible ..... Form 8
  Williston Golden susceptible.
    J. W. S. resistant ..... Form 2
    J. W. S. susceptible ..... Form 9

TABLE 1.—*Reactions of pure-line selections from 9 differential varieties of Linum usitatissimum to 14 physiologic forms of Melampsora lini as determined in greenhouse tests at Fargo, N. Dak., 1935* [1]

Physiologic form	Types of rust infection and reactions of differential hosts								
	Buda (C. I. 270)			Williston Golden (C. I. 25)			Williston Brown (C. I. 803)		
	Infection type		Host reaction	Infection type		Host reaction	Infection type		Host reaction
	Range	Predominant		Range	Predominant		Range	Predominant	
1	0 to 1+	1−	R+	0 to 1	1	R+	3	3	S
2	1 to 3	3	S−	3 to 4	3	S+	3− to 3	3	S
3	1− to 3−	3−	SR	1− to 1	1	R+	3− to 3	3	S
4	3 to 4	3	S+	1− to 1	1	R+	3	3	S
5	0 to 1−	0	R+	1 to 1+	1+	R−	3	3	S
6	1− to 1	1	R+	3 to 4	3	S+	3	3	S
7	1 to 1+	1	R+	1− to 1	1	R+	3− to 3	3−	S−
8	3	3	S	1− to 1	1	R+	3	3	S
9	1+ to 3	3	S−	1+ to 3	3	S−	3	3	S
10	0	0	I	0 to 1	0	R+	1 to 3−	2	SR
11	0 to 1−	0	R+	3 to 4	3	S+	3	3	S
12	1 to 3	3	S−	1 to 1+	1	R	3	3	S
13	1+ to 3	3	S−	1 to 1+	1+	R−	3	3	S
14	1 to 3−	3−	SR	3	3	S	3	3	S

[1] Plus and minus signs indicate somewhat greater or lesser amount of rust than the nearest figure representing the infection type, and the letters signify the following: R, resistant; S, susceptible; SR, semiresistant; and I, immune.

EXPLANATORY LEGEND FOR PLATE 1

Infection types produced by *Melampsora lini* on selected varieties of cultivated flax, *Linum usitatissimum*.

A, Type 0. No uredia produced, but chlorotic to necrotic areas formed in inoculated portions of the leaves. Akmolinsk, C. I. 515, inoculated with form 4.

B, Type 1. Small uredia formed usually in association with chlorosis of the surrounding leaf tissue. Williston Golden, C. I. 25, inoculated with form 1.

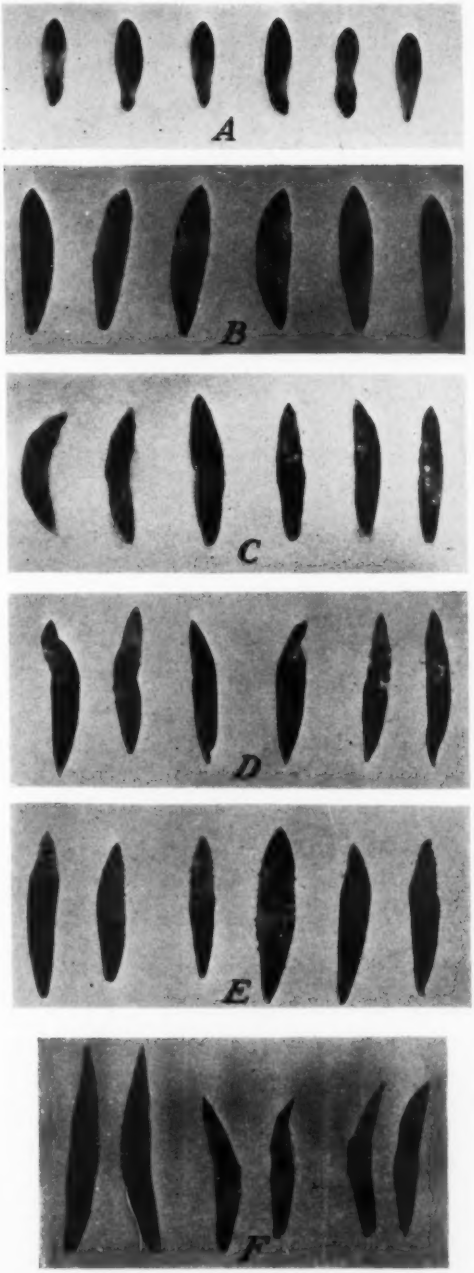
C, Type 2. Small to medium uredia of subnormal development surrounded by sharply defined necrotic areas. Williston Brown, C. I. 803, inoculated with form 10.

D, Type 3−. Isolated uredia, large and well developed but not compound, surrounded by a chlorotic area which may become necrotic; heavily infected portions of the leaves are chlorotic with arrested uredial development. Buda, C. I. 270, inoculated with form 3.

E, Type 3. Uredia large and well developed but not compound; considerable chlorosis in heavily infected areas, but uredial development only slightly retarded. Williston Golden, C. I. 25, inoculated with form 2.

F, Type 4. Uredia large and, if isolated, compound with but slight chlorosis except in the older infections. Bison, C. I. 389, inoculated with form 2.

A to *E*, × 1.5; *F*, natural size.



FOR EXPLANATORY LEGEND SEE OPPOSITE PAGE.

TABLE 1.—*Reactions of pure-line selections from 9 differential varieties of Linum usitatissimum to 14 physiologic forms of Melampsora lini as determined in greenhouse tests at Fargo, N. Dak., 1935*—Continued.

Physiologic form	Types of rust infection and reactions of differential hosts								
	Akmolinsk (C. I. 515)			J. W. S. (C. I. 708)			"Very pale blue crimped" (C. I. 647)		
	Infection type		Host reaction	Infection type		Host reaction	Infection type		Host reaction
	Range	Predominant		Range	Predominant		Range	Predominant	
1	0 to 1−	0	R+	0	0	I	3− to 3	3	S
2	0 to 1−	0	R+	0	0	I	3− to 3	3	S
3	3 to 4	3	S+	0	0	I	3− to 3	3	S
4	0 to 1	1−	R+	0	0	I	3− to 3	3	S
5	3 to 4	3	S+	0	0	I	1 to 3−	3−	SR
6	0 to 1	1−	R+	0	0	I	3− to 3	3	S
7	3 to 4	3	S+	3	3	S	2 to 3	3	S−
8	3 to 4	3	S+	0	0	I	3	3	S
9	0	0	I	3 to 4	3	S+	3	3	S
10	0	0	I	0	0	I	3− to 3	3	S
11	0 to 1	1−	R+	0	0	I	0	0	I
12	0 to 1−	0	R+	0	0	I	3− to 3	3	S
13	0	0	I	3 to 4	3	S+	3− to 3	3	S
14	0	0	I	0	0	I	2 to 3	3	S−

Physiologic form	Types of rust infection and reactions of differential hosts								
	Kenya (C. I. 709)			Argentine (C. I. 705)			Abyssinian (C. I. 701)		
	Infection type		Host reaction	Infection type		Host reaction	Infection type		Host reaction
	Range	Predominant		Range	Predominant		Range	Predominant	
1	0 to 1	1−	R+	1− to 3−	2+	SR	0	0	I
2	1 to 2	2	R+	2 to 3−	2+	SR	0	0	I
3	2+ to 3−	2+	SR	1− to 3−	2+	SR	1	1	R+
4	2− to 2+	2−	R	2 to 3−	2+	SR	0	0	I
5	0 to 2	0	R+	2 to 3−	2+	SR	1 to 1+	1	R+
6	0 to 2+	2−	R	2 to 3−	2+	SR	0	0	I
7	0 to 2−	2−	R+	3− to 3	3	S	1 to 1+	1	R+
8	2 to 3−	2+	SR	2 to 3−	2+	SR	3	3	S
9	2− to 2+	2−	R	2+ to 3−	2+	SR	0	0	I
10	0 to 1−	0	R+	0 to 1	0	R+	0	0	I
11	0	0	I	2 to 3−	2+	SR	0	0	I
12	2+ to 3−	2+	SR	2+ to 3−	2+	SR	0	0	I
13	2+ to 3−	2+	SR	2+ to 3−	2+	SR	0	0	I
14	0 to 2−	2−	R+	0 to 2+	2	R	0	0	I

DESCRIPTION OF FORMS

Form 1.—Differential selections of J. W. S. and Abyssinian C. I. 701 nearly immune; Buda, Williston Golden, Akmolinsk, and Kenya highly resistant; Argentine C. I. 705 semiresistant; Williston Brown susceptible. Under optimum rust conditions, Williston Golden developed infection types 1 to 1+; under suboptimum conditions it showed pronounced chlorosis and subsequent necrosis of inoculated leaf areas and an occasional pustule of type 1− to 1. Typical response of Buda, Akmolinsk, and Kenya, formation of chlorotic to necrotic areas with an occasional pustule of type 1−. Response of Argentine C. I. 705 variable; uredia usually aggregated in necrotic areas; under suboptimum rust conditions uredia dry prematurely and spore production is sparse; under optimum rust conditions uredia well developed and sporulation abundant.

Form 2.—Buda susceptible; Williston Golden very susceptible, and J. W. S. nearly immune. Uredia on Buda medium in size, numerous, sporulation abundant; stems and cotyledons show no resistant reaction; heavily infected leaves become chlorotic and prematurely dry.

Form 3.—Buda semiresistant; Williston Golden highly resistant; Akmolinsk very susceptible; Kenya semiresistant. Buda, uredia type 3−; variable, heavily inoculated areas necrotic with arrested pustule development, normal uredia in adjacent tissue; uredia on stem and cotyledons small but otherwise normal.

Form 4.—Buda very susceptible; Williston Golden and Akmolinsk highly resistant; Kenya resistant; J. W. S. nearly immune. Infection on Buda normal, uredia large, rarely compound, sporulation abundant, but under suboptimum conditions Buda less susceptible to form 4 than Akmolinsk to form 3 or Williston Golden to form 2. Kenya, heavily inoculated areas chlorotic to necrotic, pustules rudimentary, usually in necrotic areas at leaf margins.

Form 5.—Resistance of Buda and Kenya differentiates this form from form 3. Williston Golden slightly more susceptible than to form 3; Akmolinsk very susceptible; and J. W. S. nearly immune from both forms.

Form 6.—Buda highly resistant; Williston Golden very susceptible. Susceptibility of the "very pale blue crimped" (C. I. 647) differentiates this form from form 11.

Form 7.—Buda, Williston Golden, and Kenya very resistant; Akmolinsk very susceptible; and J. W. S. susceptible; Williston Brown semiresistant to moderately susceptible, uredia large, fewer than normal, and surrounding tissue dries prematurely. The only form producing a susceptible reaction on Argentine C. I. 705 under suboptimum conditions.

Form 8.—J. W. S. nearly immune; Williston Golden highly resistant; Buda susceptible; and Akmolinsk very susceptible. The only form that produces a susceptible reaction on Abyssinian C. I. 701.

Form 9.—Susceptibility of J. W. S. differentiates this form from form 2; Williston Golden appreciably less susceptible than to form 2.

Form 10.—Apparently the least virulent of all forms. Under suboptimum conditions Williston Brown resistant; under optimum conditions semiresistant. Buda, Williston Golden, Akmolinsk, and Kenya slightly more resistant than to form 1; Argentine C. I. 705 much more resistant.

Form 11.—The immunity of the "very pale blue crimped" (C. I. 647) differentiates this form from form 6. This is the only form to which this variety is highly resistant.

Form 12.—Kenya semiresistant, uredia large, well developed, aggregated in the heavily inoculated regions that become chlorotic and tend to dry up prematurely; Buda susceptible; Williston Golden resistant; Akmolinsk highly resistant; J. W. S. nearly immune. Differentiated from form 4 by the more susceptible reaction of Kenya and the less susceptible reaction of Buda.

Form 13.—Susceptibility of J. W. S. differentiates this form from forms 4 and 12.

Form 14.—Buda semiresistant; Williston Golden susceptible; Akmolinsk, J. W. S., and Abyssinian C. I. 701 nearly immune; Argentine C. I. 705 resistant; and Kenya very resistant. Differentiated from form 2 by semiresistance of Buda and the somewhat less susceptibility of Williston Golden.

GEOGRAPHIC DISTRIBUTION

The localities from which the 99 rust collections were obtained are shown in table 2. More than one form was obtained from several of the collections made in 1934, so that a total of 105 form identifications were made. The distribution of these forms, according to years and States or Provinces in which each was collected, is also shown in table 2.

Physiologic forms 1 to 7, inclusive, were differentiated on the reaction of three differential varieties, Buda, Williston Golden, and Akmolinsk. Since only the type specimen of each of these 7 forms was available for tests with the additional differentials used in the 1934 trials, it is possible that some of the earlier form identifications were not exact. For instance, form 9, which is distinguished from form 2 by the reaction of J. W. S., would have been classified as form 2 prior to the use of J. W. S. as a differential in 1934. Likewise, collections having pathogenic properties of form 10 would have been classed as form 1; and collections having the reactions of forms 12 and 13, as form 4.

TABLE 2.—*Geographic distribution of physiologic forms of Melampsora lini and number of times each form was isolated from Linum usitatissimum, 1931–34*

Year	Place collected [1]		Number of isolates of physiologic form—														Total number	
	State or Province	Locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Isolates	Forms
1931	Manitoba, Canada	St. Adolphe [2]	1														1	1
		Winnipeg [2]				2											2	1
		Total	1			2											3	2
	North Dakota	Cooperstown	1														1	1
		Fargo				2											2	1
		Hamilton		1													1	1
		Langdon	1		1	1											3	3
		Mandan		1													1	1
		New Salem	1														1	1
		Wishek	1			1											2	2
		Total	4	2	1	4											11	4
	Total		5	2	1	6											14	4
1932	Minnesota	Cooncreek [3]		2		1											3	2
		Lamberton	1														1	1
		Morris				1											1	1
		Northfield		1													1	1
		St. Paul			1												1	1
		Tyler	1														1	1
		Waseca															1	1
		Willmar			1												1	1
		Total	2	3	3	2											10	4
	North Dakota	Carrington			1												1	1
		Cavalier	1														1	1
		Cooperstown			1		1										2	2
		Grafton		1													1	1
		Hurdsfield	1	1													2	2
		Langdon		1													1	1
		Lawton				1											1	1
		Mandan				2											2	1
		Valley City	1														1	1
		Total	3	3	2	3	1										12	5
	South Dakota	Watertown			1												1	1
	Total		5	6	6	5	1										23	5

[1] Unless stated otherwise, collections were made by H. H. Flor. [2] 1 collection was made by F. J. Greaney. [3] 1 collection of physiologic form 2 was made by C. C. Allison.

TABLE 2.—*Geographic distribution of physiologic forms of Melampsora lini and number of times each form was isolated from Linum usitatissium, 1931–34*—Continued

Year	Place collected		Number of isolates of physiologic form —														Total number	
	State or Province	Locality	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Isolates	Forms
1933	Minnesota	Alexandria			1												1	1
		Cooncreek					1										1	1
		Crookston		1	1												2	2
		Fergus Falls						1									1	1
		Melrose		1													1	1
		Osakis	1														1	1
		Total	1	2	2		1	1									7	5
	North Dakota	Cavalier				1											1	1
		Fargo	2	2		1											5	3
		Finley	1	2													3	2
		Grafton					1										1	1
		Grand Forks					1										1	1
		Lakota				2											2	1
		Langdon		1													1	1
		Minto			1												1	1
		Pekin					1										1	1
		St. Thomas					1										1	1
		Total	3	5	1	4	4										17	5
	Oregon	Astoria [4]							1								1	1
	Total		4	7	3	4	5	1	1								25	7

1934	Minnesota	Ada														2	2	1
		Alexandria	2														2	1
		Averill	1														1	1
		Borup				1											1	1
		Brandon					1				1						2	2
		Breckenridge		1			1										2	2
		Cooncreek [3]											1				1	1
		Crookston	2			1											3	2
		Eldred					1							1	1		3	3
		Fergus Falls														3	3	1
		Northcote [4]		1	1												2	2
		Owatonna						1						1			2	2
		Waseca		1			1										2	2
		Windom	1		1							1					3	3
		Total	6	3	2	2	4	1			1	1	1	2	1	5	29	12
	North Dakota	Argusville					1										1	1
		Casselton														1	1	1
		Fargo	2											1		1	4	3
		Hillsboro		1	1		1				1			1			5	5
		Leonard														2	2	1
		Total	2	1	1		2				1			2		4	13	7
	Oregon	Corvallis [4]								1							1	1
	Total		8	4	3	2	6	1		1	2	1	1	4	1	9	43	13
1931–34	Manitoba		1			2											3	2
	Minnesota		9	8	7	4	5	2			1	1	1	2	1	5	46	12
	North Dakota		12	11	5	11	7				1			2		4	53	8
	Oregon								1	1							2	2
	South Dakota				1												1	1
	Grand total		22	19	13	17	12	2	1	1	2	1	1	4	1	9	105	14

[3] 1 collection of physiologic form 2 was made by C. C. Allison.
[4] Collected by B. B. Robinson.
[5] Physiologic forms 2 and 3 were collected by C. C. Allison.

A number of physiologic forms of flax rust are widely disseminated throughout the flaxseed-producing area of Minnesota, North Dakota, South Dakota, and Manitoba. Forms 1, 2, and 4 apparently were most prevalent during this 4-year period, but the limited number of collections studied scarcely warrants drawing definite conclusions concerning the relative prevalence of the different forms. Apparently, forms 3 and 5 also were wide-spread, as each was secured from several widely separated localities. Form 6 was obtained from only 2 collections, 1 from Fergus Falls, Minn., in 1933, and the other from Owatonna, Minn., in 1934. Only two collections were obtained outside the flaxseed-producing area. One of these, collected at Astoria, Oreg., yielded form 7 and the other, gathered near Corvallis, Oreg., gave form 8. These two forms are very distinct from all those collected in the flaxseed area and also from each other. In 1934, forms 10, 11, and 13 were each obtained but once; form 9, twice; form 12, 4 times; and form 14, 9 times. Forms 12 and 14 were found in widely scattered localities in Minnesota and North Dakota. The latter form was obtained from more collections in 1934 than was any other.

Several forms have been obtained from the same locality, although the number of collections made in each has been rather limited. Forms 1, 2, 4, 12, and 14 have been obtained from 11 collections made near Fargo, N. Dak.; forms 1, 2, 3, and 4, from 5 collections made near Langdon, N. Dak.; forms 2, 4, 5, and 11, from 5 collections made at Cooncreek (near Anoka), Minn.; and forms 2 and 4, from 3 collections made at Mandan, N. Dak.

HOST RANGE AND VARIETAL RESISTANCE

The results of inoculating 165 varieties of flax with physiologic forms 1 to 5, inclusive, are given in table 3. As only 13 of the 165 varieties tested gave indications of being rust differentials, the reaction of each variety to each form has not been tabulated separately. The varieties have been grouped according to the flax type to which they belong. The percentages of plants of each variety that were immune, resistant, or susceptible are given, as is also the general rust reaction of each variety.

TABLE 3.—*Reaction of varieties of Linum usitatissimum to five forms of Melampsora lini*

Group and variety	C. I. no.	Immune	Resistant	Susceptible	General rust reaction[1]
Linum usitatissimum crepitans (dehiscent flax):		*Percent*	*Percent*	*Percent*	
From Siberia	295	0	0	100	S
From Germany	496	0	0	100	S
From Ukraine	506	0	0	100	S
Do	507	0	0	100	S
L. usitatissimum (seed flax):					
Petals, broad, flat:					
Abyssinian:					
F. P. I.[2] 37086	36	0	0	100	S
F. P. I. 58762	300	0	0	100	S
F. P. I. 58764	302	3	9	88	S
From Egypt	380	12	9	79	S
From Fergana, S. E. Turkistan	511	0	56	44	D
F. P. I. 60559	701	48	10	42	D
From Kenya, East Africa	707	0	0	100	S

[1] Letters indicate the various types of rust reaction, as follows: D, differential variety (not reacting similarly to all forms); I, immune (75 percent or more of the plants immune); M, mixed (less than 75 percent of the plants falling into any 1 class); R, resistant (75 percent or more of the plants resistant); S, susceptible (75 percent or more of the plants susceptible).

[2] F. P. I. refers to accession number of the Division of Plant Exploration and Introduction.

TABLE 3.—*Reaction of varieties of Linum usitatissimum to five forms of Melampsora lini*—Continued

Group and variety	C. I. no.	Immune	Resistant	Susceptible	General rust reaction
		Percent	*Percent*	*Percent*	
L. usitatissimum (seed flax)—Continued.					
Petals, broad, flat—Continued.					
American:					
Blue-flowered:					
Bison	389	0	0	100	S
Blanc	323–c	0	0	100	S
Bolley No. 1823	754	9	0	91	S
Buda	270	0	54	46	D
Do	326	0	0	100	S
Diadem	321	2	31	67	D
Linota	244	0	0	100	S
Minnesota 24–410	421	0	0	100	S
Minnesota 25–202	447	0	0	100	S
Minnesota 25–221	423	0	0	100	S
Minnesota 25–245	446	0	0	100	S
Minnesota 281	438	0	0	100	S
North Dakota Resistant 5	411	0	0	100	S
North Dakota Resistant 52	275	0	0	100	S
North Dakota Resistant 114	489	0	0	100	S
North Dakota Resistant 714	399	0	0	100	S
North Dakota Resistant 726	412	0	3	97	S
North Dakota 40016	428	0	0	100	S
Pale blue	387–1	0	0	100	S
Redwing	320	0	0	100	S
Do	458	0	2	98	S
Do	499	0	51	49	D
Slope	274	0	0	100	S
Walsh	645	85	15	0	I
Winona	481	0	0	100	S
White-flowered:					
Ottawa white-flowered	24	0	0	100	S
Pink-flowered:					
Bolley Golden	644	70	30	0	M
Bolley No. 1821	751	100	0	0	I
Bolley No. 1822	750	100	0	0	I
Lethbridge Golden	23	5	5	90	S
Long No. 4	400	0	0	100	S
Long No. 66	337	0	0	100	S
Do	719	0	0	100	S
Long No. 83	354	0	0	100	S
Pale pink	173–1	0	100	0	R
Do	173–3	0	100	0	R
Do	649	0	100	0	R
Williston Golden	25	0	56	44	D
Argentine:					
North Dakota 1742	342	97	0	3	I
Minnesota 25–343	417	90	1	9	I
Minnesota 25–341	462	100	0	0	I
Minnesota 25–362	472	100	0	0	I
Minnesota 25–330	690	100	0	0	I
Minnesota 25–361–1	691	100	0	0	I
Minnesota 27–379–3	692	100	0	0	I
Minnesota 25–323	705	88	12	0	D
Biglow	414	97	0	3	I
Capa	720	21	53	26	M
Do	721	100	0	0	I
Do	722	94	6	0	I
Kenya	706	96	4	0	I
Do	709	80	18	2	D
Light mauve	379–1	24	76	0	R
Lino Grande	381–2	52	45	3	M
Long No. 5	466	94	6	0	I
Malabrigo	346	96	4	0	I
Do	696	100	0	0	I
Rio	280	100	0	0	I
Rosario	316	3	97	0	R
Indian:					
Howard and Khan (*15*):					
var. *luteum*, type 1		0	0	100	S
var. *cyaneum*, type 8		0	0	100	S
var. *purpureum*, type 11		5	0	95	S
var. *albidum*, type 12		34	0	66	M
var. *album*, type 15		0	0	100	S
var. *agreste*, type 22		0	0	100	S
var. *meridionale*, type 25		0	0	100	S
var. *pratense*, type 28		0	0	100	S
var *minor*, type 29		100	0	0	I
var. *pulchrum*, type 34		100	0	0	I
var. *commune*, type 46		100	0	0	I
var. *commune*, type 48		100	0	0	I

TABLE 3.—*Reaction of varieties of Linum usitatissimum to five forms of Melampsora lini*—Continued

Group and variety	C. I. no.	Immune	Resistant	Susceptible	General rust reaction
L. usitatissimum (seed flax)—Continued.					
Petals, broad, flat—Continued.					
Indian—Continued.					
Howard and Kahn (*13*)—Continued.		*Percent*	*Percent*	*Percent*	
var. *commune*, type 53		99	0	1	I
var. *commune*, type 55		0	99	1	R
var. *campestre*, type 68		99	1	0	I
var. *sativum*, type 121		41	59	0	M
Shaw, Khan, and Alam (*19*), type 124	710	29	71	0	M
Mediterranean:					
Beladi	377	75	25	0	I
Crete	31–1	57	28	15	M
Cyprus	680	55	4	41	M
Giza	378	100	0	0	I
Morocco	376–2	96	0	4	I
Russian:					
Akmolinsk	515	11	15	74	D
Do	520	17	3	80	D
Billings	184	2	2	96	S
Crimean	563	27	5	68	M
Damont	3	99	0	1	I
Fergana	512	0	0	100	S
Newland	188	96	3	1	I
North Caucasian	620	45	13	42	M
Novelty	140	0	19	81	S
Pale blue	176	5	95	0	R
Samarkand	514	5	16	79	D
Winter:					
Roman winter	470	40	8	52	M
Hybrid:					
Reserve × Morye	486	19	25	56	M
Saginaw × Ottawa 770 B	675	100	0	0	I
Do	676	100	0	0	I
Do	677	100	0	0	I
Winona × Ottawa 770 B	651	100	0	0	I
Do	652	100	0	0	I
Do	653	100	0	0	I
Do	654	92	0	8	I
Do	656	100	0	0	I
Do	657	100	0	0	I
Do	658	98	0	2	I
Do	660	3	0	97	S
Do	661	97	1	2	I
Do	662	100	0	0	I
Do	664	100	0	0	I
Do	667	100	0	0	I
Do	671	100	0	0	I
Do	672	100	0	0	I
Do	673	100	0	0	I
Do	674	100	0	0	I
Do	681	100	0	0	I
Do	682	100	0	0	I
Do	697	100	0	0	I
Do	711	2	34	64	M
Do	716	100	0	0	I
La Plata	324	91	5	4	I
Long No. 125	356	40	0	60	M
North Dakota 40046	492	93	4	3	I
Tammes light blue	332	100	0	0	I
Tammes pale blue	333	97	0	3	I
Petals, narrow, margins crimped:[3]					
Ecru-olive[4] seed	325	0	0	100	S
Minnesota 25–125	392	0	0	100	S
Minnesota 29–39	684	100	0	0	I
Minnesota 29–55	685	24	0	76	S
Minnesota 29–76	686	100	0	0	I
Minnesota 29–45	687	100	0	0	I
Ottawa 770 B	355	100	0	0	I
Ottawa 829 C	391	0	0	100	S
Pale blue	646	4	9	87	S
Tammes crimped	330	0	0	100	S
"Very pale blue crimped"	647	5	31	64	D

[3] The word "crimped" is here used to describe the petal margins, which are incurved and somewhat wavy.

[4] RIDGWAY, R. COLOR STANDARDS AND COLOR NOMENCLATURE. 43 pp., illus. Washington, D. C. 1912.

TABLE 3.—*Reaction of varieties of Linum usitatissimum to five forms of Melampsora lini*—Continued

Group and variety	C. I. no.	Immune	Resistant	Susceptible	General rust reaction
L. usitatissimum (fiber flax):					
Petals, narrow, margins crimped—Continued.					
Blue-flowered:		*Percent*	*Percent*	*Percent*	
Althausen	628	0	0	100	S
Do	630	7	0	93	S
Dalgonetz	498	0	0	100	S
F. I. No. 3	604	2	6	92	S
J. W. S.,[1] F. P. I. 73560	388	3	8	89	S
J. W. S.	708	16	0	84	D
Peerless	695	1	0	99	S
Saginaw	449	7	3	90	S
White-flowered:					
Friesland white	56–1	0	0	100	S
Minnesota 25–64	420	0	0	100	S
Pinnacle	693	0	2	98	S
Saginaw white	448	0	0	100	S
Tammes white	329	0	0	100	S
Tammes yellow seed	331	0	0	100	S
Pink-flowered:					
Deep pink	648	0	0	100	S
Pale pink	479	0	0	100	S
Tall pink	451–3	0	1	99	S
Do	451–3	0	0	100	S
Tammes deep pink	334	0	0	100	S
Do	336	0	0	100	S

[1] J. W. S. are the initials of J. W. Stewart, the originator of the variety.

When 75 percent or more of the tested plants in a variety fell into a single reaction class, the variety, if not differential, was thought to possess the reaction of that class; when less than 75 percent of the tested plants fell into a single reaction class, the variety was considered as too heterogeneous to be classified and was termed "mixed." Approximately twelve 30-day-old plants of each variety were inoculated with each rust form, and in cases where the classification was in doubt the tests were repeated. The percentage figures, therefore, are based on the reaction of 60 or more plants.

The lack of genetic purity of the varieties for rust reaction was one of the striking features of this test. Thirty-nine varieties were pure for rust immunity, but twenty-two of these were Minnesota hybrids that had been selected particularly for this quality. Twenty-two additional varieties had from 75 to 99 percent of the plants immune. Twenty of these were classed as immune and two as differentials. In a majority of the varieties included in this group most of the plants lacking immunity were highly resistant. Fifty-three varieties were pure for susceptibility. An additional 22 had from 75 to 99 percent of their plants susceptible. Nineteen of these were classed as susceptible and three as differentials. Seven varieties were classed as resistant, 3 of which were pure for resistance and 3 showed plants either resistant or immune. Fourteen varieties were so heterogeneous that they could not be classified as to predominance of reaction, and were classed as mixed. Additional differentials might have been obtained from this last group, but their reactions to the five forms did not indicate them to be such. Thirteen varieties were found to contain rust-differentiating strains, and were classed as differential varieties.

The varieties and strains included in this test do not exhaust the possibilities for obtaining immune, resistant, or susceptible lines in any of the groups. These varieties were chosen because they were

typical of the different groups and of diverse geographical origin or because they possessed commercial possibilities, and they probably are representative of their respective groups in regard to rust reaction. The dehiscent flaxes, *Linum usitatissimum* var. *crepitans*, were pure for rust susceptibility. This was the only major group in which all varieties and strains were consistently pure for one type of rust reaction. The American blue-flowered and white-flowered seed flaxes and the white-flowered and pink-flowered fiber flaxes were predominantly susceptible, but some varieties in both of these groups possessed plants that were either resistant or immune. The Abyssinian varieties and the blue-flowered fiber flaxes also were predominantly susceptible, but most of the varieties in these groups were mixtures in which some plants were either resistant or immune. The Saginaw × Ottawa 770 B hybrids were pure for immunity. The Winona × Ottawa 770 B hybrids and the Mediterranean and Argentine varieties were predominantly immune, but a number of varieties in these groups possessed plants the reactions of which ranged from complete immunity to extreme susceptibility. The other hybrids and the Russian varieties were heterogeneous in reaction, most varieties in these two groups having plants falling into all three rust-reaction categories. Varieties with petal margins crimped were relatively pure for rust reaction.

STABILITY OF PHYSIOLOGIC FORMS

Physiologic forms 1 to 4 of *Melampsora lini* have been in culture for approximately 4 years and have passed through 20 to 30 urediospore generations. In none of these forms nor in any of the others that have been studied has there been any indication of a change in pathogenicity.

DISCUSSION

The effect of the discovery of physiologic forms of *Melampsora lini* on measures to control this rust through the development and use of resistant varieties is, of course, problematical. Thus far, 14 physiologic forms have been distinguished by the reaction of seven differential hosts. It seems probable that more forms will be isolated when additional differentials are discovered and when more rust collections are studied. Allen (*1*) has shown that *M. lini* is heterothallic. The importance of this phenomenon in the origin of new forms of flax rust is not yet known. However, it has been demonstrated (*16*, *22*) that the aecial stage on the barberry is a fertile field for the development of new physiologic forms of *Puccinia graminis tritici* Eriks. and Henn. Since the process of aecial formation in the two rusts is comparable, there is no reason to believe that new forms of *M. lini* may not originate in the aecial stage on flax. The destruction of the common barberry, the aecial host of *P. graminis* Pers., would effectively prevent the production of new forms of *P. graminis* by hybridization. *M. lini*, however, is a eu-autoecious rust, and therefore to preclude the opportunity for the development of new rust forms through hybridization would necessitate the complete destruction of all rusted portions of flax plants from previous crops, an impracticable task.

Although *Melampsora lini* appears to be highly specialized, not only on various other species of *Linum* (*5*, *8*, *9*, *17*), but, as has been demonstrated by the present tests, on *L. usitatissimum*, and although it possesses abundant opportunities for hybridization and the subsequent development of new forms, the prospects of rust control through the development of resistant varieties appear to be bright. The 165 varieties of flax showed surprisingly little specific response to five forms of flax rust. This is the more remarkable when it is considered that these 165 varieties represented the fruit of a systematic effort to obtain diverse types of *L. usitatissimum* from all parts of the world. Of the 165 varieties, 152 gave no indication of possessing rust-differentiating potentialities. Sixty-one varieties were predominantly immune from all five forms with which they were tested. Since these immune varieties comprised a number of flax types, and since Henry (*10*) has shown that immunity from flax rust is transferred independently of wilt resistance or morphologic type, there should be no lack of immune breeding material.

The breeding program, already in progress, for the development of rust-resistant varieties of flax, appears to rest on a sound basis. Henry (*10*) found Ottawa 770 B and certain strains of Williston Golden and Argentine to be immune from rust. In the present investigations, certain forms of rust were found to attack all strains of Williston Golden, but Ottawa 770 B and certain Argentine selections have been consistently immune. Henry used only the latter two as rust immune parents in his breeding work, and most of the Minnesota selections that have been derived from these crosses were immune from the five forms of rust with which they were tested. Thus far, there has been no evidence of the existence of a form of flax rust capable of attacking Ottawa 770 B, certain Argentine selections or varieties possessing similar factors for resistance. Nevertheless, it would be desirable to subject these immune varieties to rust collections from other parts of the world to determine whether forms capable of attacking them exist. Stakman, Levine, and Bailey (*21*) found White Tartar oats resistant to all forms of *Puccinia graminis avenae* Eriks. and Henn. collected in North America, but susceptible to forms of this rust obtained from Sweden and South Africa. If forms of *Melampsora lini* capable of attacking the immune flax varieties of the United States exist in other parts of the world, measures should be taken to assure their exclusion from this country, since it has been demonstrated that teliospores on bits of straw and chaff that are often present with the seed are carriers of flax rust (*10*).

The heterogeneous rust reaction of so many of the varieties was surprising. Apparently natural hybridization plays a more important role than has sometimes been supposed (*4*) or else the nursery technique is at fault. It appears more probable that the former is the case. Henry and Tu (*12*) found, under conditions at St. Paul, Minn., that natural crossing between varieties in adjacent rows or even in rows several feet apart was too important a factor to be neglected. Apparently, this condition prevails in other localities, since 70 of the 165 varieties studied gave heterogeneous rust reaction. Bagging of individual plants and isolation of the separate varieties in the field may be necessary in order to insure the maintenance of varietal purity. It is possible that a test to determine rust reaction, made in conjunction with the certification of rust-resistant varieties, would aid materially in maintaining varietal purity.

SUMMARY

Strains of Buda (C. I. 270), Williston Golden (C. I. 25), Williston Brown (C. I. 803), Akmolinsk (C. I. 515), J. W. S. (C. I. 708), Kenya (C. I. 709), "very pale blue crimped" (C. I. 647), Argentine (C. I. 705), and Abyssinian (C. I. 701) have been selected as differential varieties for the identification of physiologic forms of *Melampsora lini* (Pers.) Lév. on *Linum usitatissimum* L.

From 99 collections of *Melampsora lini* made in the United States and Canada, 14 physiologic forms have been distinguished by the reaction of the differential varieties named above.

Several forms of the rust were found to be widely distributed in Minnesota, North Dakota, South Dakota, Oregon, and Manitoba. In several localities more than one form was found.

In the 4-year period covered by these investigations four rust forms have passed through 20 to 30 urediospore generations without any apparent change in pathogenicity.

Pathogenicity tests indicated that as a rule flax varieties are not specific in their reaction to the different forms of rust. Of 165 varieties tested, only 13 gave differential reactions to five forms.

Pathogenicity tests showed that many varieties were not pure lines in respect to rust reaction. Lines pure for this characteristic have been readily obtained by a process of plant selection.

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INTRACAPSULARY BOLLS IN ASIATIC COTTON[1]

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INTRODUCTION

The presence of an abnormal growth in cotton bolls, which was interpreted as a formation of supernumerary carpels, was reported by Meade [2] in 1913 and described as follows:

> In its simplest form the abnormality consisted of a solid, elongated, whitish body, developed in the center of the boll between the placentae. In many instances, however, this body was divided into from two to five longitudinal compartments, resembling miniature locks, which inclosed rudimentary ovules. In some cases it extended nearly the entire length of the boll, but was always unattached except at the base.

One upland cotton boll was observed by Meade at Clarksville, Tex., in which this abnormal growth was sufficiently developed to form a small rudimentary boll containing two apparently mature seeds.[3]

At the United States Acclimatization Garden, Bard, Calif., in 1932 and 1933, numerous rudimentary bolls were observed in the bolls of a strain of *Gossypium herbaceum* L. introduced from Tashkent, Uzbek, Union of Soviet Socialist Republics. These rudimentary bolls are described in the present paper. No observations were made of the bolls produced by this strain of cotton prior to 1932, but simple forms of the abnormal growth were present in a few of the bolls saved for herbarium specimens during 1930 and 1931. Simple forms of this abnormality were also observed in the bolls of two other strains of *G. herbaceum* and in a few bolls of *G. davidsoni* Kellogg grown in the same field in 1932. Numerous bolls were examined in 1932 and 1933 of other strains of *G. herbaceum*, *G. hirsutum* L., *G. barbadense* L., *G. nanking* Meyen, *G. neglectum* Tod., and several other species of cotton, but no indication of this abnormal growth was observed. However, simple forms of this abnormality have been observed frequently in varieties of upland cotton in other localities and in a few bolls of *G. barbadense* at Glendale, Calif.[2]

The term "supernumerary carpels" does not adequately describe this abnormal growth when it reaches such a stage of development that small rudimentary bolls are formed. Therefore, in this paper the term "supernumerary carpels" has been applied to the simple forms of this growth (fig. 1, *A*), and the term "intracapsulary bolls" has been used in cases where the growth was sufficiently developed to form small rudimentary bolls (fig. 1, *C*).

[1] Received for publication July 1, 1935; issued January 1936.

[2] MEADE, R. N. SUPERNUMERARY CARPELS IN COTTON BOLLS. U. S. Dept. Agr., Bur. Plant Indus. Circ. 111: 25–28, illus. 1913.

[3] A study of supernumerary carpels, in relation to the general morphology of the cotton boll, has been made by W. W. Ballard, of the Bureau of Plant Industry. (Unpublished data.)

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DESCRIPTION OF INTRACAPSULARY BOLLS

Fourteen intracapsulary bolls were found on the five plants of *Gossypium herbaceum* growing at Bard, Calif., in 1932, and all closely resembled in color and structure the normal bolls in which they were produced. The outer tissue was rather thin but was dotted with numerous oil glands. Some of the intracapsulary bolls were of normal shape, but others were somewhat lop-sided from being pressed against the placentae of the bolls in which they were produced. They appeared, from the outer surface, to be divided into 2, 3, or 4 carpels, but when broken were found to consist of only a single carpel containing from 1 to 3 mature seeds. The placentae were not sufficiently developed to form separate carpels, and the seeds were attached near the base of the bolls. In a few cases a very slender structure was observed to extend upward from the apex of the intracapsulary bolls; this probably had the function of a style and conducted the pollen to the ovules.

The seeds, which were slightly rounder and in some instances larger than those produced in the normal bolls, were covered with the usual coating of short fuzz, and all but two had lint that ranged from 12 to 24 mm in length. Ten of the nineteen seeds that developed in the intracapsulary bolls germinated when planted in 1933 and produced normal healthy plants. In addition to the seeds, a number of rudimentary ovules were developed in the intracapsulary bolls and supernumerary carpels.

The size of bolls, number of seeds per boll, number of boll divisions, and the length and quality of lint in the intracapsulary bolls and in normal bolls are given in table 1. Figure 1 shows the various stages of development in the bolls.

TABLE 1.—*Size of bolls, number of seeds per boll, number of boll divisions, and length and quality of lint in intracapsulary bolls and in normal bolls of Gossypium herbaceum at Bard, Calif., 1932*

Boll no.	Size of bolls		Seeds per boll	Boll divisions	Length of lint	Quality of lint
	Diameter	Length				
	Mm	*Mm*	*Number*	*Number*	*Mm*	
1	6	9	1	2	-------	No lint.
2	8	10	1	2	-------	Do.
3	10	9	1	3	23	Fairly strong.
4	9	11	1	2	22	Very weak.
5	12	11	2	4	16	Very weak and sparse.
					17	Do.
6	7	10	1	3	15	Do.
7	14	17	3	4	17	Do.
					20	Do.
					20	Do.
8	8	10	1	3	19	Do.
9	7	11	1	2	24	Fairly strong.
10	13	15	2	4	19	Very weak and sparse.
					19	Do.
11	11	13	1	3	18	Do.
12	11	14	2	4	20	Fairly strong.
					21	Do.
13	12	12	1	4	17	Do.
14	8	10	1	3	12	Very weak and sparse.
Mean for normal bolls	27	25	18-30	3-5	25	Generally soft and not very strong.

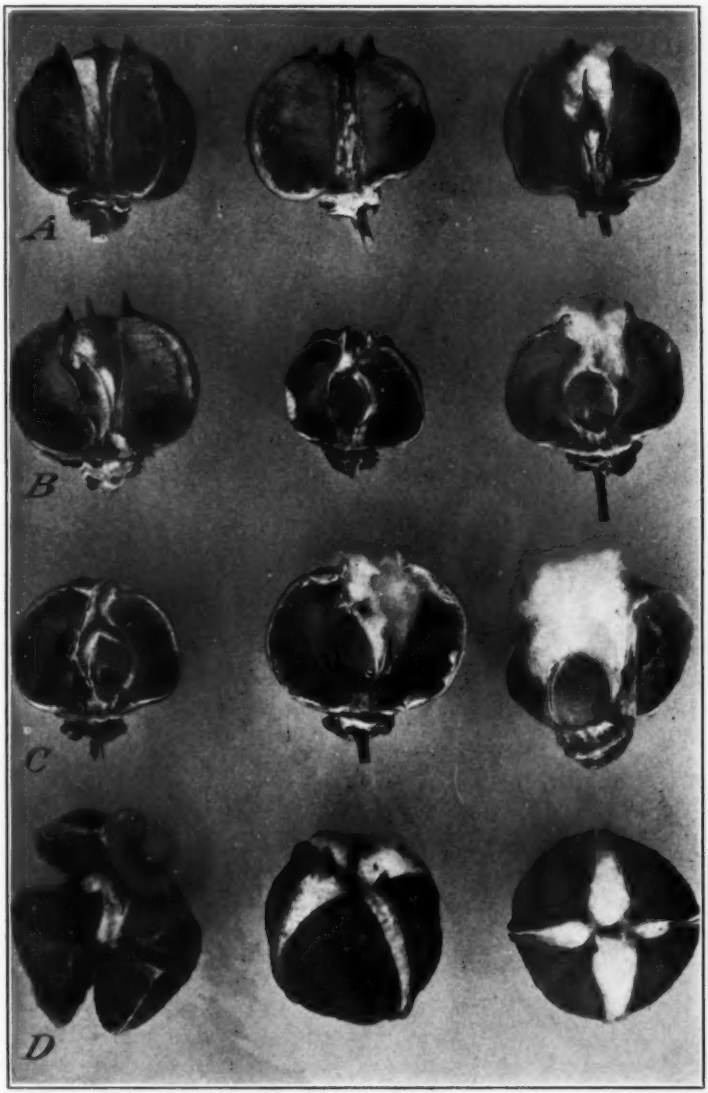

FIGURE 1.—Bolls of *Gossypium herbaceum* showing various stages of development of supernumerary carpels from (*A*) the simplest form to (*C*) the intracapsulary bolls. Two normal bolls of this strain are shown at the right in *D*.

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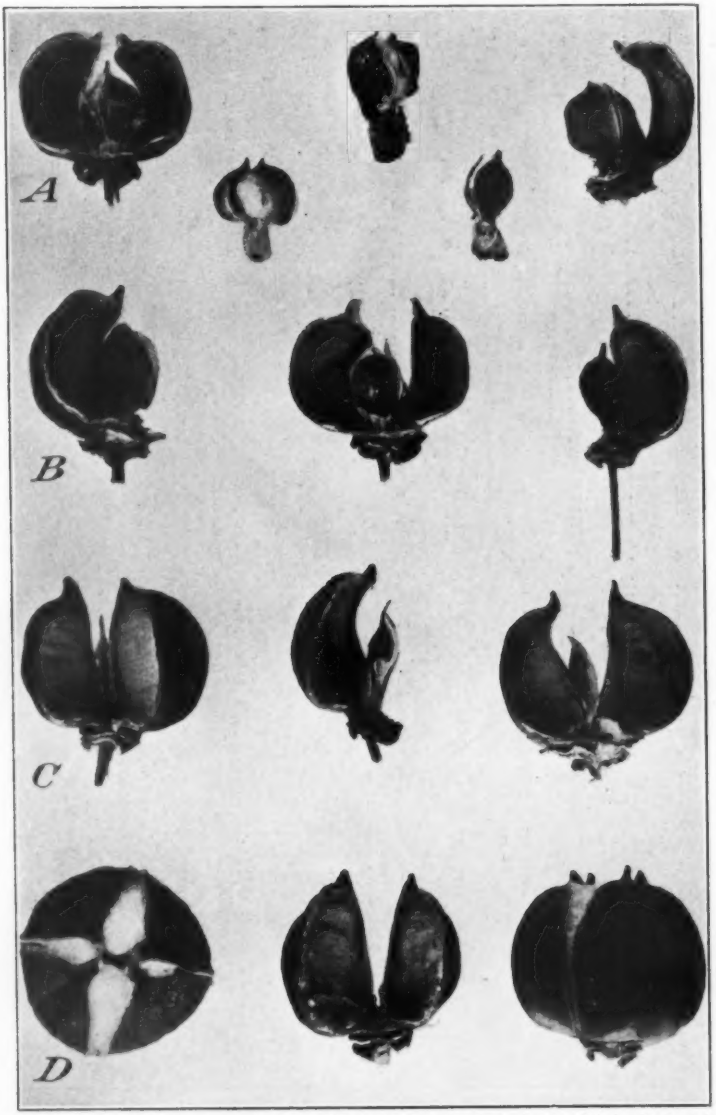

FIGURE 2.—Bolls of *Gossypium herbaceum* with seed cotton removed, showing (*A*) detached, and (*B* attached, intracapsulary bolls, (*C*) supernumerary carpels, and (*D*) normal bolls.

Figure 2 shows bolls with seed cotton removed. As viewed from outside, 4 of the intracapsulary bolls appeared to be divided into 2 carpels, 5 into 3 carpels, and 5 into 4 carpels. Ten bolls contained 1 mature seed each, 3 contained 2 seeds each, and 1 had 3 seeds. On the 17 seeds that produced lint, the shortest lint was 12 mm and the longest 24 mm. The smallest intracapsulary boll was 6 mm in diameter and 9 mm in length, and the largest was 14 mm in diameter and 17 mm in length. The normal bolls of this strain have from 3 to 5 carpels and produce 18 to 30 seeds with lint averaging 25 mm in length. The normal bolls average 27 mm in diameter and 25 mm in length. It will be noted from these measurements that the normal bolls are broader than long, whereas 11 of the 14 intracapsulary bolls were longer than they were broad. This was probably due to the fact that the intracapsulary bolls could develop more easily along the placentae of the bolls that contained them than they could expand against the placentae. The placentae in some of the bolls were pressed back, forming a crescent or half circle, by the development of the intracapsulary bolls.

OBSERVATIONS IN 1933

Observations were made in 1933 with the strain of *Gossypium herbaceum* from Tashkent to ascertain (1) what effect seasonal changes have on the development of supernumerary carpels and intracapsulary bolls, (2) whether the frequency of supernumerary carpels and intracapsulary bolls changes as acclimatization proceeds, and (3) whether the abnormal growth character is hereditary. For these observations the 1932 plants were ratooned in the spring of 1933, and additional plantings were made on April 13 with original seed from Tashkent and with seed acclimatized 1, 2, and 3 years at Bard. A planting with seed acclimatized 2 years at Bard was also made at the United States Acclimatization Field Station, State College, N. Mex.[4]

The seed acclimatized 1 year was produced during 1930, and the seed acclimatized 2 years was produced during 1931 from the 1930 seed grown at Bard. The planting made in 1933 with these two seed stocks was from random samples. The seed acclimatized 3 years was produced in 1932 from the seed grown at Bard in 1930 and 1931, and the seed used in the 1933 planting was from the intracapsulary bolls produced in 1932.

EFFECTS OF SEASONAL CHANGES AND ACCLIMATIZATION

The seed planted April 13, 1933, germinated readily and the seedlings made rapid growth. The plants began flowering in June and continued until October. The first bolls matured in August and the last in November. The 1932 plants were ratooned in March 1933 and by May had begun flowering, which continued until October. The first bolls on these plants matured in July and the last in November.

In order to determine the effect of seasonal changes on the presence and development of the abnormal growth character, the period during which the bolls matured was divided into four 30-day periods. During the first period, July 4 to August 3, the ratooned plants matured 261 bolls, of which 50, or 19.15 percent, contained supernumerary carpels. No bolls were matured during this period by the

[4] Planting was made and data were collected by A. R. Leding, chief scientific aid.

plants of the 1933 planting. During the second period, August 4 to September 3, supernumerary carpels were present in 36 percent of the bolls matured on the ratooned plants and in 42.1, 42.7, 42.2, and 41.2 percent of the bolls matured on the plants grown in 1933 from the original imported seed and from seed representing 1, 2, and 3 years of acclimatization, respectively. Not only did the percentages of bolls containing supernumerary carpels increase during the third and fourth periods, from September 4 to October 4 and from October 5 to November 4, but the abnormal growth was considerably more developed, a total of 130 intracapsulary bolls being produced. These data (table 2) were recorded collectively for all plants of each seed stock, but no plants were observed that did not produce a fairly high percentage of such bolls.

TABLE 2.—*Effects of seasonal changes and acclimatization on number of bolls containing supernumerary carpels and intracapsulary bolls at Bard, Calif., 1933*

Seed stock	Year planted	Plants	Period of maturity	Bolls			Bolls containing supernumerary carpels and intracapsulary bolls
				Total	With supernumerary carpels	Intracapsulary	
		Number		*Number*	*Number*	*Number*	*Percent*
Original seed imported from Union of Soviet Socialist Republics.	[1] 1932	5	July 4–Aug. 3	261	50	0	19.15
			Aug. 4–Sept. 3	211	76	0	36.0
			Sept. 4–Oct. 4	188	131	10	75.0
			Oct. 5–Nov. 4	86	69	9	90.6
Do	1933	3	Aug. 4–Sept. 3	76	32	0	42.1
			Sept. 4–Oct. 4	125	90	8	78.4
			Oct. 5–Nov. 4	107	81	13	87.9
1-year acclimatized seed	1933	9	Aug. 4–Sept. 3	173	74	0	42.7
			Sept. 4–Oct. 4	265	205	15	83.1
			Oct. 5–Nov. 4	422	323	41	86.3
2-year acclimatized seed	1933	6	Aug. 4–Sept. 3	64	27	0	42.2
			Sept. 4–Oct. 4	84	66	5	84.5
			Oct. 5–Nov. 4	99	76	11	87.9
3-year acclimatized seed	1933	6	Aug. 4–Sept. 3	83	36	0	41.2
			Sept. 4–Oct. 4	71	53	5	81.7
			Oct. 5–Nov. 4	189	148	13	85.2

[1] The 1932 plants were ratooned in the spring of 1933.

The increase in the number of supernumerary carpels as the season advanced and the development of the extreme intracapsulary boll stage during the latter part of the season indicate that differences in conditions during the season influence this abnormal development.

Data collected on the seven plants observed at State College, N. Mex., in 1933 showed that of a total of 340 bolls which matured 172 contained supernumerary carpels and 3 contained intracapsulary bolls with one mature seed each. The percentage of bolls containing supernumerary carpels and intracapsulary bolls for these seven plants varied from 28.5 to 65.8 percent, with a mean of 51.5 percent.

No difference was noted in the degree of development of the supernumerary carpels and intracapsulary bolls produced by the plants grown from the original seed stock and from seed representing 1, 2, and 3 years acclimatization at Bard, nor were there any significant differences in the percentages of bolls that contained this abnormal growth.

The number of intracapsulary bolls having 2, 3, or 4 boll divisions and the number having 1, 2, or 3 mature seeds are given in table 3.

TABLE 3.—*Number of intracapsulary bolls with 2, 3, or 4 divisions and number of these bolls containing 1, 2, or 3 mature seeds, Bard, Calif., 1933*

Seed stock	Year of planting	Intracapsulary bolls with indicated number of—					
		Boll divisions			Seeds per boll		
		2	3	4	1	2	3
		Number	*Number*	*Number*	*Number*	*Number*	*Number*
Original seed imported from Union of Soviet Socialist Republics	[1] 1932	3	13	3	15	4	0
Do	1933	6	13	2	19	2	0
1-year acclimatized seed	1933	14	38	4	49	6	1
2-year acclimatized seed	1933	3	12	1	14	2	0
3-year acclimatized seed	1933	4	11	3	14	3	1

[1] The 1932 plants were ratooned in the spring of 1933.

HEREDITARY CHARACTER

The observations made at Bard, Calif., and at State College, N. Mex., indicate that in the strain of *Gossypium herbaceum* from Tashkent abnormal boll growth is a hereditary character, but apparently it is of such a nature that its expressions are largely influenced by environmental conditions. The effect of environment is shown by the increase in the percentage of bolls that produced supernumerary carpels and the development of intracapsulary bolls as the season advanced.

SUMMARY

The presence of supernumerary carpels in cotton bolls is not an uncommon abnormality in most types and strains of cultivated cottons. Usually the growth is limited to a white slender body extending through the center of the boll from the base almost to the apex. However, at Bard, Calif., in 1932 and 1933, this abnormal growth was observed in various degrees of development in a large proportion of the bolls of a strain of *Gossypium herbaceum* introduced from Tashkent, Uzbek, Union of Soviet Socialist Republics. In some of the bolls the growth was developed to the extent of forming small intracapsulary bolls containing from 1 to 3 mature seeds which were covered with lint of fair quality.

These intracapsulary bolls closely resembled the bolls in which they were contained in appearance, color, and shape. As viewed from outside they appeared to be divided into 2 to 4 carpels, but the placentae were not sufficiently developed to form separate carpels.

The abnormal boll growth observed in this strain of *Gossypium herbaceum* appears to be a hereditary character, but of such a nature that its expression is largely influenced by environmental conditions. The environmental effects are shown by the increase in the percentage of bolls containing supernumerary carpels and in the development of intracapsulary bolls as the season advanced.

A METHOD FOR ESTIMATING THE VOLATILE SULPHUR CONTENT AND PUNGENCY OF ONIONS[1]

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INTRODUCTION

In studying the effect of various ecological conditions on the pungency of onions it became necessary to develop a method by means of which pungency could be measured more accurately than can be done by the ordinary tasting test.

It is generally known that onions and other members of the genus *Allium* owe their pungency and particular taste to an essential oil that is specific for each species. The volatile oil of *Allium cepa L.* was first investigated by Semmler[2] in 1892. He demonstrated the extremely high degree of pungency by showing that this oil occurs in onions in a concentration of only about 0.005 percent. After distilling 5,000 kg of onions he was able to obtain only 233 g of the crude oil. Determining some of the physical constants and the chemical composition of the crude oil, Semmler showed that the principal constituent of the oil is allyl-propyl-disulphide

$$\begin{matrix} C_3H_7-S \\ | \\ C_3H_5-S. \end{matrix}$$

The crude oil was found to contain 43.37 percent of sulphur, while the sulphur content of pure allyl-propyl-disulphide is 43.26 percent. Although Semmler studied some of the chemical properties of onion oil he did not develop any analytical procedure by which the oil could be measured quantitatively in different lots of onions.

DEVELOPMENT OF THE METHOD

A relatively simple method for determining the volatile sulphur in plants was proposed by Peterson.[3] According to this method a stream of air is passed through a wide U tube containing the plant tissue and heated to 100° C. The volatile sulphur is carried away by the air stream and is absorbed in a tube containing copper oxide filings which are thus reduced to copper sulphate. After the copper sulphate crystals have been dissolved the sulphate is determined by precipitation with barium chloride.

In order to test the dependability of this method two lots of 500 g of finely cut onion tissue were dried in a ventilated oven at 60° and at 100° C. for 24 hours. The dried residue was then hydrolyzed and the amount of volatile sulphur which remained was determined by

[1] Received for publication July 25, 1935; issued January 1936. Contribution 130 from Department of Vegetable Crops, New York (Cornell) Agricultural Experiment Station.

[2] SEMMLER, F. W. DAS AETHERISCHE OEL DER KUECHENZWIEBEL (ALLIUM CEPA L.). Arch. der Pharm. 230: 443–448. 1892.

[3] PETERSON, W. H. FORMS OF SULFUR IN PLANT MATERIALS AND THEIR VARIATION WITH THE SOIL SUPPLY. Jour. Amer. Chem. Soc. 36: 1290–1300. 1914.

the distillation method described later. It was found that heating at 60° had removed only 77.7 percent of the volatile sulphur originally present, and that heating at 100° had removed 88.3 percent. While this method may give dependable results with other plant tissues which are relatively low in volatile sulphur, it is obvious that it cannot be used to measure the pungency of onions.

Realizing the close chemical relationship between onion oil and mustard oil, the writer next investigated a method proposed by Dircks [4] and improved by Schlicht [5] which has become a standard method for the determination of mustard oil in rapeseed cakes. In this procedure the oil is first liberated from the glucoside by acid hydrolysis, then distilled into a solution of alkaline permanganate which readily oxidizes the sulphides of the oil to sulphate. The excess of permanganate is destroyed by the addition of alcohol, the precipitate of manganese dioxide is filtered off, and the sulphate is precipitated from the clear, acidified filtrate with barium chloride.

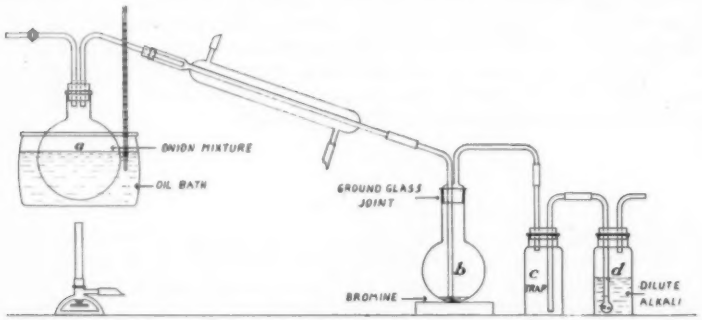

FIGURE 1.—Apparatus used in the determination of volatile sulphur in onions: *a*, 2-liter round-bottom, short-neck flask; *b*, 1-liter round-bottom flask containing 5 cc of bromine and 5 cc of water; *c*, trap; *d*, flask containing dilute sodium hydroxide for absorbing bromine fumes driven off during heating.

In applying this method to the determination of volatile sulphur in onions it was found that, while the results were satisfactory if proper precautions were taken, it was difficult to remove all traces of the manganese dioxide precipitate from the filtrate and also to prevent partial reduction of the sulphate after the addition of alcohol.

In an attempt to eliminate some of the difficulties encountered in using this method several other oxidizing agents were tried, and finally it was found that when the onion oil is distilled directly into saturated bromine water the sulphides present are rapidly oxidized to sulphate. The excess of bromine is easily driven off by heating, the small sulphur-free residue is filtered off, and the sulphate is precipitated from the filtrate with barium chloride. As compared with the permanganate method this procedure not only gave more accurate results but also required considerably less time. The details of this method are as follows:

Select a representative sample of at least 20 onions. Take one-fourth or one-half of each bulb and slice these sections into slices not

[4] DIRCKS, V. ÜBER DAS VORKOMMEN DER MYRONSÄURE UND DIE BESTIMMUNG DES DARAUS GEBILDETEN SENFÖLS IN DEN SAMEN DER CRUCIFEREN UND IN DEN ÖELKUCHEN. Landw. Vers. Sta. 28: [179]–200. 1883.

[5] SCHLICHT, A. EIN BEITRAG ZUR BEURTEILUNG DER RAPSKUCHEN NACH IHREM SENFÖLGEHALT. Landw. Vers. Sta. 41: [175]–190, illus.

thicker than one-half centimeter. Mix the material and weigh out exactly 500 g. Transfer the sliced material to a 2-liter, round-bottom, short-neck flask (fig. 1, *a*). Add 100 cc of concentrated hydrochloric acid and 250 cc of water. Submerge the flask in an oil bath to the level of the onion mixture and connect with a straight-tube condenser. To the lower end of the condenser attach a delivery tube which reaches to the bottom of a 1-liter, round-bottom flask (*b*) containing 5 cc of bromine and 5 cc of water. An outlet tube from the receiving flask leads to a trap (*c*) and from there to a flask (*d*) containing dilute sodium hydroxide to absorb bromine fumes which may be driven off during heating.

Heat the oil bath until it has reached a temperature of 122° to 124° C. Maintain at this temperature for 3 hours. During this period distillation should proceed very slowly and about 200 cc of the distillate should collect in the receiving flask *b*. At the end of 3 hours remove flask *a* containing the onion mixture from the oil bath; cool, and add 500 cc of water and 300 g of sodium chloride. While rotating the flask vigorously, add slowly, not more than 10 cc at a time, enough 50-percent sodium hydroxide almost to neutralize the mixture (about 95 cc) using litmus paper as an indicator. Again connect the flask to the condenser, heat the oil bath to 135°, maintain at this temperature for 1 hour, then raise the temperature to 145° and distill until 800 cc have collected in the receiving flask. Rinse the condenser and the delivery tube, stopper the receiving flask, and allow it to stand overnight. Add a few glass beads and heat very slowly on a Kjeldahl digestion rack or under a hood until all the bromine has been driven off. Transfer the distillate to a 1-liter beaker and evaporate on a steam bath to a volume of about 300 cc, or until the solution has become clear. Filter, wash the filter paper, and add 10 cc of bromine water to the filtrate. Heat on a hot plate or steam bath to drive off the excess of bromine and evaporate to a volume of about 300 cc. While still hot add, drop by drop, stirring vigorously, 10 cc of a 10-percent solution of barium chloride. Continue heating for 10 minutes. Cool, allow to stand overnight, filter through ashless filter paper, and wash the precipitate until free from chlorides. Ignite the precipitate and filter and weigh as barium sulphate. Make a blank determination if the reagents contain an appreciable amount of sulphur.

Precautions: All rubber tubing and stoppers used in the distilling apparatus should first be boiled in dilute alkali and then washed thoroughly to remove any adherent sulphur bloom. It is preferable to make connections by means of interchangeable ground-glass joints. This is almost essential for the connection between the delivery tube and the receiving flask (*b*). Where connections are made with rubber tubing the glass tubes should fit together as closely as possible to expose only a minimum of rubber to the bromine. Rubber stoppers can be protected effectively by a coat of acid-resistant stopcock grease.

A second outlet from the distilling flask (*a*) provided with a stopcock is useful in preventing possible sucking back of the distillate when the boiling flask is cooled.

EXPERIMENTAL RESULTS

In the following experiments, which were carried out in order to study the effect of modifying certain details of the procedure it was necessary to exclude the factor of individual variability of the sample. This was done conveniently by slicing 12 or more bulbs, thoroughly mixing the material, and weighing out 2 or 3 aliquots of 500 g each which were analyzed by slightly different methods.

EFFECT OF HYDROLYSIS ON THE YIELD OF VOLATILE SULPHUR

At the outset of the experiment it was noticed that the distillation of onion oil proceeds extremely slowly unless the heated material is first hydrolyzed with dilute hydrochloric acid. This suggests strongly that onion oil, like mustard oil, occurs in the bulb in the form of a glucoside which has to undergo hydrolysis before the oil can be distilled off. Table 1 shows that if hydrolysis is carried out by heating 500 g of sliced onions with 100 cc of concentrated hydrochloric acid and 250 cc of water, hydrolysis is complete within 3 hours. Where the hydrolysis was omitted prior to distillation the amount of sulphur in the first 800 cc of the distillate was reduced to less than one-fifth. On the other hand, extending the period of hydrolysis to 6 hours failed to give a higher yield of sulphur than was obtained after 3 hours hydrolysis.

TABLE 1.—*Effect of hydrolysis on the yield of volatile sulphur*

Sample	Sulphur in first 800 cc of distillate from 500 g of onions after—		
	No hydrolysis	3-hour hydrolysis	6-hour hydrolysis
	Milligram	*Milligram*	*Milligram*
A	7.9	56.1	56.3
B	9.3	56.5	55.8

EFFECT OF HYDROGEN-ION CONCENTRATION ON THE YIELD OF SULPHUR IN THE DISTILLATE

Before the hydrolyzed oil can be distilled it is necessary partly to neutralize the mixture in order to prevent the distillation of appreciable quantities of hydrochloric acid which may later interfere with the proper precipitation of the sulphate. However, since protein sulphur is readily hydrolyzed in alkaline solution it is important to keep the mixture faintly acid. Table 2 shows that distillation from a neutral and an acid solution gave practically identical results, whereas the yield of sulphur was increased appreciably when the distillation was carried out from an alkaline solution.

TABLE 2.—*Effect of hydrogen-ion concentration on the yield of sulphur in the first 800 cc of the distillate from 500 g of onions*

Sample	Sulphur when approximate pH of mixture at the beginning of distillation was—		
	1.3	6.5	11.1
	Milligrams	*Milligrams*	*Milligrams*
A	38.1	38.2	47.3
B	58.4	58.2	63.5

RATE OF DISTILLATION OF VOLATILE SULPHUR

The volatile sulphur is separated from the onion mixture by means of steam distillation. This process is usually slow, and in order to hasten the rate of distillation the boiling temperature of the onion mixture was raised by the addition of 300 g of sodium chloride. The temperature of the oil bath was maintained at 145° C.; a higher temperature did not seem advisable since Semmler [6] found that onion oil decomposes at a temperature of 160°. In order to determine how much of the distillate should be collected to recover all of the volatile oil present, each 250 cc was collected separately during a few experiments.

Table 3 shows that the distillation of the sulphur is still incomplete after 1,500 cc of the liquid has been distilled. However, the quantity of sulphur in the distillate becomes very small after 750 or 1,000 cc has been distilled. Nevertheless, when it is desired to determine the actual amount of volatile sulphur it would be necessary to collect 2,000 cc or more of the distillate. On the other hand, when only comparative values are sought it seems hardly worth while to distill such a large amount, especially since the rate of distillation appears to be fairly uniform for different samples of onions. The writer in his experiments arbitrarily chose 800 cc as the quantity of distillate which was to be collected for the determination of relative pungency in onions.

TABLE 3.—*Rate of distillation of the volatile sulphur*

Successive fractions of 250 cc	Sulphur in successive fractions of the distillate		Successive fractions of 250 cc	Sulphur in successive fractions of the distillate	
	Sample E	Sample F		Sample E	Sample F
	Milligrams	*Milligrams*		*Milligrams*	*Milligrams*
First	64.34	50.06	Fourth	1.21	0.65
Second	7.52	4.56	Fifth	.70	.49
Third	2.57	1.44	Sixth	.54	.36

PRECISION OF THE METHOD AND VARIABILITY OF THE SAMPLE

To obtain some idea concerning the precision of the method, as well as the variability of the sample which may be expected, a commercial lot of Yellow Bermuda onions was divided into 5 groups, each containing 10 bulbs. Each group was prepared for analysis separately,

[6] SEMMLER, F. W. See footnote 2.

and after slicing and mixing had been completed, these lots were divided again into 2 separate samples of 500 g each, designated as A and B (table 4). Differences between the analyses of A and B illustrate the precision of the method while the successive numbers of the samples signify the variability of the samples.

TABLE 4.—*Volatile sulphur determinations on 5 samples of the same lot of Yellow Bermuda onions illustrating precision of the method and variability of the sample*

Item	Sample 1		Sample 2		Sample 3		Sample 4		Sample 5		Average
	Aliquot A	Aliquot B	Aliquot A	Aliquot B	Aliquot A	Aliquot B	Aliquot A	Aliquot B	Aliquot A	Aliquot B	
Sulphur	*P.p.m.* 110	*P.p.m.* 108	*P.p.m.* 116	*P.p.m.* 117	*P.p.m.* 109	*P.p.m.* 111	*P.p.m.* 115	*P.p.m.* 116	*P.p.m.* 119	*P.p.m.* 122	114.3

Table 4 shows that in every case the error due to the variability of the sample was greater than the experimental error. Unless a greater uniformity of the sample can be assured it seems advisable to take a larger number of bulbs, perhaps 20 or 25, in order to obtain more accurate results. At any rate, it appears doubtful whether differences of less than 10 parts per million are significant. It must be realized, however, that differences in the content of volatile sulphur between samples from several varieties were as a rule very much greater. While some samples contained as little as 28 parts per million others yielded as high as 200 parts per million.

DISCUSSION

The proposed method for estimating the relative pungency of onions is based on the assumption that the onion oil has a definite composition and that differences in the pungency of onions are due solely to quantitative differences in the percentage of oil present. This assumption seems justified since Semmler found that the onion oil consists almost entirely of allyl-propyl-disulphide, a definite chemical compound. Furthermore, the writer and Knott [7] found that wherever differences in pungency could be detected by the tasting test they were associated with corresponding differences in the content of volatile sulphur.

As previously shown, during the distillation of volatile sulphur, more than 1,500 cc of the liquid must be distilled before all traces of volatile sulphur are removed from the onion mixture. It will be noticed in table 3, however, that after the first 1,000 cc have been distilled the quantity of sulphur in the subsequent portions of the distillate rapidly approaches a constant value, which in comparison with the total amount present is exceedingly small. It seems possible that these last traces of volatile sulphur are not derived from onion oil but are due to a second reaction, possibly a very slow decomposition of protein sulphur. At least, the trend of the distillation curve suggests this explanation.

The principal advantage of the proposed method is that in studying the factors determining the pungency of onions results can be expressed

[7] PLATENIUS, H., and KNOTT, J. E. PUNGENCY OF ONIONS IN RELATION TO VARIETY AND ECOLOGICAL FACTORS. Amer. Soc. Hort. Sci. Proc. (1934) 32: 593–595. 1935.

in numerical values which make it possible to compare onions of different varieties or bulbs grown under different ecological conditions. Preliminary experiments indicate that the same method, with slight modifications can be used to determine the pungency and the volatile sulphur content of garlic, cabbage, and possibly other vegetables which owe their specific taste to some volatile oil containing sulphur.

While the method itself is relatively simple it is time-consuming because of the slow process of steam distillation. Therefore it cannot be recommended as a routine method where large numbers of samples are involved.

SUMMARY

A new and relatively simple method is described for estimating the volatile sulphur content and pungency of onions. This method is based on the assumption that onion oil has a definite chemical composition, and that differences in the pungency of onions are due solely to quantitative differences in the amount of oil present and, indirectly, to the volatile sulphur content. The method possesses sufficient accuracy for the purpose, but since it involves steam distillation it is time-consuming and cannot be recommended as routine procedure when a large number of samples is involved.

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